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Contribution to the knowledge of *Choroterpes* (Ephemeroptera: Leptophlebiidae)

К познанию *Choroterpes* (Ephemeroptera: Leptophlebiidae)

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КЛЮЧЕВЫЕ СЛОВА: систематика, Ephemeroptera, Leptophlebiidae, Atalophlebomaxillata, *Choroterpes*, *Neochoroterpes*, *Euthraulus*, *Monophyllus*, *Dilatognathus*, *Choroterpides*, новые виды.

ABSTRACT. The taxon Atalophlebomaxillata is characterized by presence of an apical flange on maxilla; this flange is lost only in those representatives, whose maxillae are highly specialized. Within Atalophlebomaxillata-Atalophlebolinguata, a new tribe Choroterpini **tribus n.** (or Choroterpes/fg1) is established, to comprise *Thraulus* and *Choroterpes* s.l. (or Choroterpes/fg2). The taxon Choroterpes/fg2 is divided into Choroterpes/fg3 (characterized by lanceolate median filaments on tergalii) and Euthraulus/g1 (characterized by arched penial arms). Choroterpes/fg3 includes a widely distributed plesiomorphon Choroterpes/fg4 and a Nearctic taxon *Neochoroterpes*. Based on imagoes reared from larvae, new species and subspecies of Choroterpes/fg4 are described — *Ch.* (*Ch.*) *picteti subcostalis* **ssp.n.** from Caucasus (Russia), *Ch.* (*Ch.*) *ludmilae* **sp.n.** from Oman and *Ch.* (*Ch.*) *mercatorius* **sp.n.** from Sulawesi Island (Indonesia). The taxon Euthraulus/g1 has exclusively Old-World distribution; it includes widely distributed plesiomorphon Euthraulus/g2 and two small Oriental taxa — *Monophyllus* **subgen.n.** and *Dilatognathus* **subgen.n.** Based on imagoes reared from larvae, a new species of Euthraulus/g2 is described — *Ch.* (*Euthraulus*) *caucasicus* **sp.n.**, and additional descriptions to *Ch.* (*E.*) *altioculus*, *Ch.* (*E.*) *sumbarensis* and *Ch.* (*E.*) *signatus* are given. The taxon *Monophyllus* includes a single species *Ch.* (*Monophyllus*) *monophyllus* **sp.n.**, described as mature larvae from Hainan Island (China). Larvae of the taxon *Dilatognathus* are known under the generic name *Choroterpides*, whose type species (*exiguus* Eaton, 1884 [*Thraulus*]) is known only as imago and probably belongs to Euthraulus/g2. The type species of *Dilatognathus* is *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.**, described as imagoes reared from larvae in Lombok Island (Indonesia). Similar modifications in mouthparts structure independently evolved in non-related taxa *Dilatognathus*, *Notophlebia*, Hermanellognatha, Hagenulus/fg3 and Ulmeritus/g2.

РЕЗЮМЕ. Таксон Atalophlebomaxillata характеризуется наличием апикальной пластинки на максилле; эта пластинка утрачена только у тех представителей, максиллы которых сильно специализированы. В составе Atalophlebomaxillata–Atalophlebolinguata выделяется новая триба Choroterpini **tribus n.** (или Choroterpes/fg1), объединяющая *Thraulus* и *Choroterpes* s.l. (или Choroterpes/fg2). Таксон Choroterpes/fg2 делится на Choroterpes/fg3 (характеризующийся ланцетовидным медиальным филаментом тергалий) и Euthraulus/g1 (характеризующийся дуговидными руками пениса). Choroterpes/fg3 включает широко распространённый плезиоморфон Choroterpes/fg4 и неарктический таксон *Neochoroterpes*. По имаго, выведенным из личинок, описываются новые виды и подвиды Choroterpes/fg4 — *Ch.* (*Ch.*) *picteti subcostalis* **ssp.n.** с Кавказа (Россия), *Ch.* (*Ch.*) *ludmilae* **sp.n.** из Омана и *Ch.* (*Ch.*) *mercatorius* **sp.n.** с о. Сулавеси (Индонезия). Таксон Euthraulus/g1 известен исключительно из Старого Света; он включает широко распространённый плезиоморфон Euthraulus/g2 и два маленьких ориентальных таксона — *Monophyllus* **subgen.n.** и *Dilatognathus* **subgen.n.** По имаго, выведенным из личинок, описывается новый вид Euthraulus/g2 — *Ch.* (*Euthraulus*) *caucasicus* **sp.n.**, а также даются дополнительные описания *Ch.* (*E.*) *altioculus*, *Ch.* (*E.*) *sumbarensis* и *Ch.* (*E.*) *signatus*. Таксон *Monophyllus* включает единственный вид *Ch.* (*Monophyllus*) *monophyllus* **sp.n.**, описанный по зрелым личинкам с о. Хайнань (Китай). Личинки *Dilatognathus* известны под родовым названием *Choroterpides*, типовой вид которого (*exiguus* Eaton, 1884 [*Thraulus*]) известен только по имаго и, вероятно, относится к Euthraulus/g2. Типовым видом *Dilatognathus* **subgen.n.** является *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.**, описанный по имаго, выведенным из личинок на о. Ломбок (Индонезия). Сход-

ные преобразования в строении ротовых частей независимо произошли у неродственных таксонов *Dilatognathus*, *Notophlebia*, Hermanellognatha, Hagenulus/fg3 и Ulmeritus/g2.

Introduction

This paper continues revision of mayfly system based on the principles of cladoendesis [Kluge & Novikova, 2011; Kluge, 1912] with usage of the dual nomenclature system [Kluge, 2010]. Based on these principles, instead of the formal subfamily Atalophlebiinae, a series of subsequently subordinated rank-free taxa have been established: Atalophleboadentata (or Atalophlebia/fg1) > Atalophlebopectinata (or Atalophlebia/fg2) > Atalophleboculata (or Atalophlebia/fg3) > Atalophlebomaxillata (or Atalophlebia/fg4) > Atalophlebolinguata (or Atalophlebia/fg5) [Kluge, 2004, 2008, 2009]. The phylogenetic relationships within the taxon Atalophlebolinguata remain poorly known. Within Atalophlebolinguata, a subordinated holophyletic taxon Hagenulus/fg1 has been established [Kluge, 2008].

In the present paper, based on new material, the taxon Atalophlebomaxillata is redefined and a new holophyletic taxon Choroterpes/fg1 within Atalophlebolinguata is established. Classification of the taxa discussed in this paper is the following:

1. Atalophlebomaxillata
1.1. Atalophlebolinguata
1.1.1. Choroterpes/fg1 (incl. *Thraulus*)
1.1.1.1. Choroterpes/fg2 (incl. *Euthraulus*)
1.1.1.1.1. Choroterpes/fg3 (incl. *Neochoroterpes*)
1.1.1.1.1.1. Plesiomorphon Choroterpes/fg4
1.1.1.1.1.1-1. Choroterpes/fg4 *picteti* [*Choroterpes*]
1.1.1.1.1.1-1.1. Choroterpes/fg4 *p. picteti* [*Choroterpes*]
1.1.1.1.1.1-1.2. Choroterpes/fg4 *p. subcostalis* **ssp.n.** [*Choroterpes*]
1.1.1.1.1.1-2. Choroterpes/fg4 *nigrescens* [*Choroterpes*]
1.1.1.1.1.1-3. Choroterpes/fg4 *ludmilae* **sp.n.** [*Choroterpes*]
1.1.1.1.1.1-4. Choroterpes/fg4 *mercatorius* **sp.n.** [*Choroterpes*]
1.1.1.1.1.2. Neochoroterpes/g(1), or *Neochoroterpes*
1.1.1.1.1.2-1. Neochoroterpes/g(1) *oklahoma* [*Choroterpes*]
1.1.1.1.2. Euthraulus/g1 (incl. *Monophyllus*, *Dilatognathus*)
1.1.1.1.2.1. Plesiomorphon Euthraulus/g2
1.1.1.1.2.1-1. Euthraulus/g2 *altioculus* [*Choroterpes*]
1.1.1.1.2.1-2. Euthraulus/g2 *sumbarensis* [*Choroterpes*]
1.1.1.1.2.1-3. Euthraulus/g2 *caucasicus* **sp.n.** [*Choroterpes*]
1.1.1.1.2.1-4. Euthraulus/g2 *signata* [*Cloe*]
1.1.1.1.2.1-5. Euthraulus/g2 *bugandensis* [*Euthraulus*]
1.1.1.1.2.2. Monophyllus/g(1), or *Monophyllus* **subgen.n.**
1.1.1.1.2.2-1. Monophyllus/g(1) *monophyllus* **sp.n.** [*Choroterpes*]
1.1.1.1.2.3. Dilatognathus/g(1), or *Dilatognathus* **subgen.n.**
1.1.1.1.2.3-1. Dilatognathus/g(1) *cataractae* **sp.n.** [*Choroterpes*]
1.1.1.1.2.3-2. Dilatognathus/g(1) sp.1
1.1.1.1.2.3-3. Dilatognathus/g(1) sp.2
1.1.1.1.2.3-4. Dilatognathus/g(1) sp.3
1.1.1.1.2.3-5. Dilatognathus/g(1) sp.4

All material, including holotypes and paratypes of new species, will be permanently deposited in the Zoological Institute of Russian Academy of Sciences (Saint Petersburg, Russia), but is temporarily located in the Department of Entomology of Saint Petersburg State University. In the lists of material examined, the following arbitrary signs are used: **L** — larva; **S** — subimago; **I** — imago; **L-S-I♂** — male imago reared from larva, with larval and subimaginal exuviae; **L-S-I♀** — female imago reared from larva, with larval and subimaginal exuviae; **L-S♂** — male subimago reared from larva, with subimaginal exuviae; **L/S♂** — male subimago extracted from mature larva.

1. Atalophlebomaxillata, or **Atalophlebia/fg4**

Systematic position: Leptophlebia/fg1—Atalophleboadentata—Atalophlebopectinata—Atalophleboculata—Atalophlebomaxillata.

Circumscriptional name: Atalophlebomaxillata Kluge, 2009.

Hierarchical typified name: Atalophlebia/fg4 (sine *Terpides*; incl. *Castanophlebia*).

Possible rank-based name:

— subfamily Atalophlebiinae s.l.

Autapomorphies.

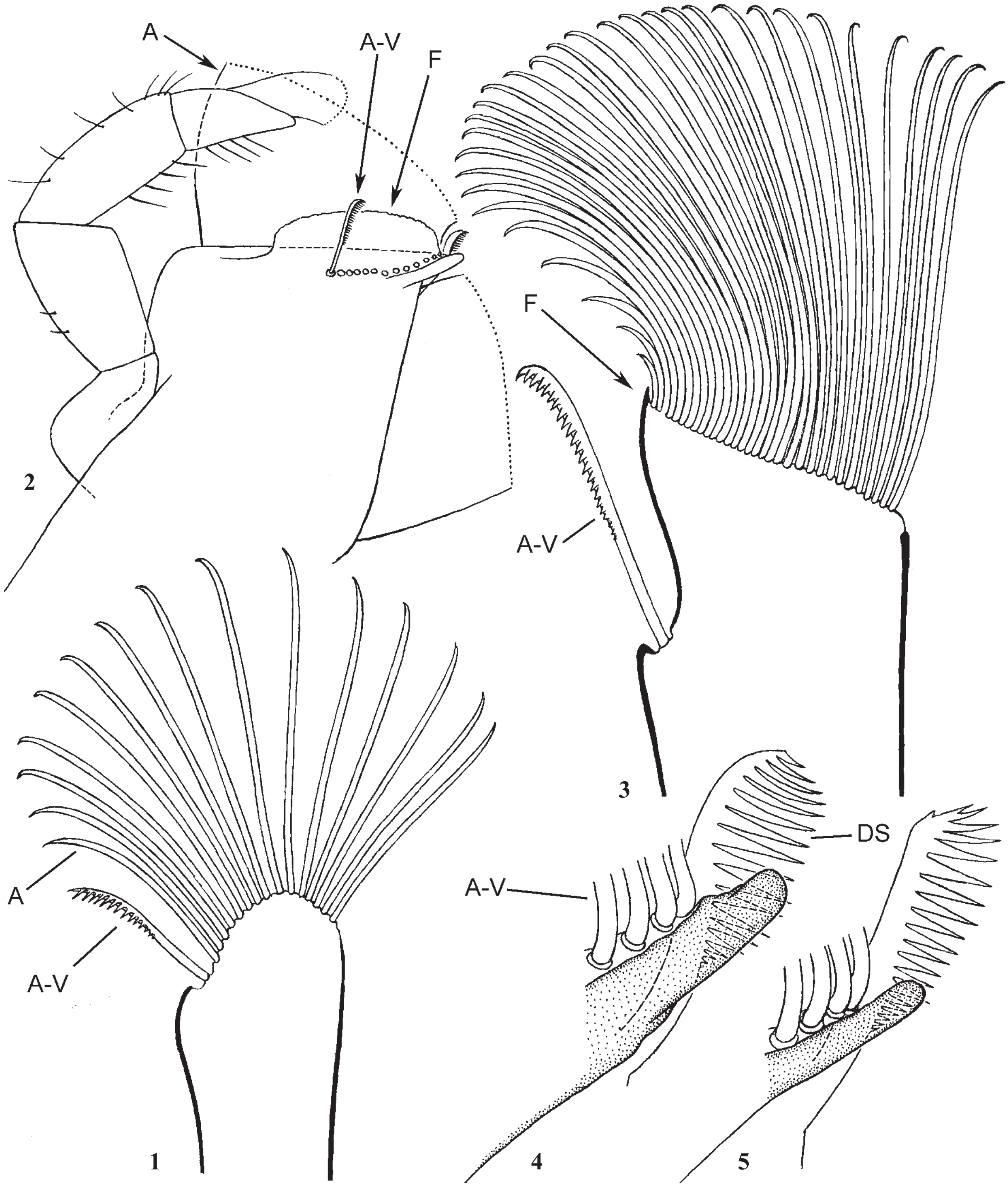
(1) Maxilla has an **apical flange**, which represent a continuation of its ventral wall to apical direction and separates the apical field of long filtering setae (characteristic for Leptophlebia/fg1) from the apical-ventral row of pectinate setae (also characteristic for Leptophlebia/fg1); thanks to the apical flange, the apical field of long filtering setae is shifted to the dorsal side of maxilla and its ventral margin locates far from the apical-ventral row of pectinate setae (Fig. 3). The apical flange reaches inner margin of maxilla, and laterally terminates fare from outer margin of maxilla (Fig. 2). The apical flange is very thin and translucent, so it is poorly visible on background of dense apical filtering setae. In my previous paper maxilla of *Farrodes bimaculatus* Peters & Alayo, 1971 was shown wrongly, without the apical flange [Kluge, 1994: Fig.4]; actually it has the apical flange similar to that in Fig. 2.

Among the taxa examined, the apical flange is reduced only in taxa with highly specialized maxillae of the «*Dilatognathus*-like type» — Hermanellognatha [Kluge, 2008: Fig. 37], *Notophlebia* Peters & Edmunds, 1970, *Hagenulus morrisonae* Peters & Alayo, 1971 (but not *Hagenulus caligatus* Eaton, 1882) and last instar larva of *Dilatognathus* **subgen.n.** (Fig. 129) (but not its younger larvae — Fig. 132).

Unlike Atalophlebomaxillata, in other Leptophlebia/fg1 (i.e., Terpides/fg1, Habrophlebia/fg1, Calliarcys/fg(1) and the plesiomorphon Leptophlebia/fg2) the apical flange is absent, the apical field of long filtering setae is located at most on ventral side of maxilla, and its ventral margin is located close to the apical-ventral row of pectinate setae (Fig. 1) [Kluge, 2009: Fig.1].

(2) Distal dentiseta is usually lost, so maxilla has a single pectinate dentiseta (which is originally the proximal one) (Figs 2, 4, 5).

Discussion. In the previous papers [Kluge, 2008, 2009] I characterized the taxon Atalophlebia/fg4, or Atalophlebomaxillata, by a single autapomorphy — loss of the distal dentiseta. However, *Aprionyx* Barnard, 1940 has the distal dentiseta retained; its distal dentiseta is somewhat smaller than in Terpides/fg1 and can be poorly visible, being pressed to the dense apical filtering setae. At the same time, hypopharynx of *Aprionyx* has a pair of processes typical for Atalophlebolinguata. Some individuals of Atalophlebomaxillata have the single dentiseta bifurcate, with a slender non-pectinate distal branch; possibly, this branch is a vestige of the distal dentiseta basally fused with the proximal dentise-



Figs 1–5. Maxilla. 1 — *Terpides* (*Fittkaulus*) *amazonicus* Kluge, 2009, transverse section of maxilla through apical field of long filtering setae and apical-ventral row of pectinate setae; 2–4 — *Choroterpes* (*Choroterpes*) *picteti subcostalis* **sp.n.**: 2 — ventral view (most part of setae not shown, areas occupied by them shown by dotted lines; instead of pectinate setae of apical-ventral row, their bases are shown); 3 — transverse section of maxilla through apical field of long filtering setae and apical-ventral row of pectinate setae; 4 — medio-apical projection, ventral view (dotted); 5 — *Ch.* (*Ch.*) *picteti picteti*, the same. **A** — apical field of long filtering setae; **A-V** — pectinate seta of apical-ventral row; **DS** — dentiseta; **F** — apical flange.

Рис 1–5. Максилла. 1 — *Terpides* (*Fittkaulus*) *amazonicus* Kluge, 2009, поперечный срез максиллы через апикальное поле длинных фильтрующих щетинок и апикально-вентральный ряд гребенчатых щетинок; 2–4 — *Choroterpes* (*Choroterpes*) *picteti subcostalis* **sp.n.**: 2 — вентрально (большая часть щетинок не показана, занимаемые области показаны точечными линиями; вместо гребенчатых щетинок апикально-вентрального ряда показаны их основания); 3 — поперечный срез максиллы через апикальное поле длинных фильтрующих щетинок и апикально-вентральный ряд гребенчатых щетинок; 4 — медио-апикальный выступ, вентрально (пунктирован); 5 — *Ch.* (*Ch.*) *picteti picteti*, то же. **A** — апикальное поле длинных фильтрующих щетинок; **A-V** — гребенчатые щетинки апикально-вентрального ряда; **DS** — дентисета; **F** — апикальная пластинка.

ta; if this is so, presence of such branch is a transitional condition between presence of the distal dentiseta and its absence. The apical flange, described above, seems to be more reliable character of Atalophlebomaxillata, than the loss of distal dentiseta.

Classification. The taxon Atalophlebomaxillata is divided into a small South African taxon Castanophlebia/fg1 and a large taxon Atalophlebolinguata.

1.1. Atalophlebolinguata Kluge, 2009, or **Atalophlebia/fg5**

Systematic position: Leptophlebia/fg1—Atalophleboadentata—Atalophlebopectinata—Atalophleboculata—Atalophlebomaxillata—Atalophlebolinguata.

Circumscriptional name: Atalophlebolinguata Kluge, 2009.

Hierarchical typified name: Atalophlebia/fg5 (sine *Castanophlebia*).

Possible rank-based name:

— subfamily Atalophlebiinae s.str..

Autapomorphy. The taxon Atalophlebolinguata is characterized by presence of a pair of lateral arched processes on hypopharynx [Kluge, 2009]. These processes never undergo reduction and are retained in all representatives of Atalophlebolinguata, independently of specialization of their mouthparts.

Classification. The taxon Atalophlebolinguata includes majority of Leptophlebiidae; its phylogeny is still unclear. Among numerous taxa, which constitute Atalophlebolinguata, I had already characterized the holophyletic taxon Hagenulus/fg1 with Neotropical distribution [Kluge, 2008]. Here is characterized the taxon Choroterpes/fg1, whose distribution is mainly Old-World.

1.1.1. **Choroterpes/fg1**

Systematic position: Leptophlebia/fg1—Atalophleboadentata—Atalophlebopectinata—Atalophleboculata—Atalophlebomaxillata—Atalophlebolinguata—Choroterpes/fg1.

Hierarchical typified name: Choroterpes/fg1 (incl. *Thraulus* Eaton, 1881) [f: Choroterpini **tribus n.**; g: *Choroterpes* Eaton, 1881; type species: *Ch. lusitanica* Eaton, 1881 (synonym of *Leptophlebia picteti* Eaton, 1871)].

Possible rank-based name:

— tribus Choroterpini.

Autapomorphies.

(1) Difference between tergalius I and tergalii II–VII is more or less expressed: tergalius I tends to narrowing and simplification, while tergalii II–VII always retain both lamellae, which are widened and have additional processes (in Choroterpes/fg2 each lamella has up to three processes, in Thraulus/g1 — many processes).

In Choroterpes/fg2 the first tergalius is usually unilamellate, very narrow, thread-like, with a single non-branched trachea (Figs 6, 30, 57, 76, 98, 120); rarely wider, with trachea branched (in *nigrescens* Barnard, 1932 [*Choroterpes*]); rarely with one process (in Neochoroterpes/g(1) — Fig. 66); rarely bilamellate, with both lamellae slender and lacking processes (in *petersi* Tong et Dudgeon, 2003 [*Choroterpes*]). Sometimes the first tergalius undergoes further reduction: in *prati* Puig et Gaino, 1996 [*Choroterpes*] it is present in male, absent in female; in *Dilatognathus* **subgen.n.** it is completely lost.

In Thraulus/g1 the first tergalius usually has both lamellae slender and lacking processes; rarely consists of a single slender lamella lacking processes (in *femoratus* Li et al., 2006 [*Thraulus*]). Some species, which are regarded to be related with *Thraulus*, have the first tergalius bilamellate and similar to tergalii II–VII (*hsui* Peters et Tsui, 1972 [*Thraulus*]; *mariae* Peters et Tsui, 1972 [*Thraulus*]; *torrentis* Gillies, 1964 [*Masharikella*]).

Characters of unclear phylogenetic status.

(2) Larval patella-tibial suture is lost on all legs (Figs 24–27, 46–48, 85–87, 147–149). In contrast to larva, in imago and subimago patella-tibial suture usually retains the primitive condition, being present on middle and hind legs and absent on fore legs; among species examined, only in *oklahoma* Traver, 1934 [*Choroterpes*] imago and subimago lack patella-tibial suture on all legs, as in larva.

(3) Hind wing has Sc terminating near middle of costal margin; costal projection is expressed and varies from short and obtuse (Figs 16, 88, 106, 135–137) to stretched and pointed (Figs 40, 50). Larval hind protopteron in all cases has obtuse costal projection; if adult costal projection is stretched and pointed, it grows when wing develops from protopteron (Figs 51, 52).

Plesiomorphy.

(4) Imaginal and subimaginal claws are always ephemeropteroid.

Classification. The taxon Choroterpes/fg1 is divided into Thraulus/g1 and Choroterpes/fg2. The taxon Thraulus/g1 [g: *Thraulus* Eaton 1881: 195] includes taxa known under the generic names *Thraulus* Eaton, 1881 and *Masharikella* Peters et al., 1964. Its distribution is limited by the Old World. There are 2 European species: *bellus* Eaton, 1881 [*Thraulus*] and *thraker* Jacob, 1988 [*Thraulus*]. 3 African species: *turbinatus* Ulmer, 1909 [*Hagenulus*]; *fasciatus* Kimmins, 1956 [*Hagenulus*]; *torrentis* Gillies, 1964 [*Masharikella*]. 11 South Asian species: *bishopi* Peters et Tsui, 1972 [*Thraulus*]; *demoulini* Peters et Tsui, 1973 [*Thraulus*]; *fatuus* Kang et Yang, 1994 [*Thraulus*]; *femoratus* Li et al., 2006 [*Thraulus*]; *gopalani* Grant et Sivaramakrishnan, 1985 [*Thraulus*]; *grandis* Gose, 1980 [*Thraulus*]; *macilentus* Kang et Yang, 1994 [*Thraulus*]; *mudumalaiensis* Soman, 1991 [*Thraulus*]; *semicastanea* Gillies, 1951 [*Habrophlebiodes*]; *umbrosus* Kang et Yang, 1994 [*Thraulus*]. Besides this, I have a reared male imago and non-reared imagoes of two undescribed species of *Thraulus* from Sulawesi. The taxon Choroterpes/fg2 is characterized below.

1.1.1.1. **Choroterpes/fg2**

Figs 2–151

Systematic position: Choroterpes/fg1—Choroterpes/fg2.

Hierarchical typified name: Choroterpes/fg2 (sine *Thraulus*; incl. *Euthraulus* Barnard, 1932).

Possible rank-based names:

— tribus Choroterpini;

— genus *Choroterpes*.

Autapomorphies.

(1) Egg surface with a unique relief: there are papillae and ridges; ridges stretch from one papilla to another and form broken lines in such a manner that each papilla is surrounded by a regular crown of several (6–8) acute angles formed by these ridges; usually each such crown is elevated in a form of aster-like or flower-like protuberance (Figs 17, 20–23, 70–75, 94, 96, 97). This relief is absent in *pacis* Sartori, 1991 [*Choroterpes*] and *assimilis* Gaino et Sowa, 1985 [*Choroterpes* (*Euthraulus*)] [Gattoliat & Sartori, 2008]. In *mercatorius* **sp.n.** [*Choroterpes*] this relief is modified (Fig. 56).

(2) Each tergalius II–VII has both lamellae wide, 3-pointed, i.e. with two processes by sides of terminal process (Fig. 67, 77–82, 140, 141). Non-unique apomorphy. In selected species some lamellae have less than three apices (Figs 7–12, 31–36, 58–63, 104, 138). In *Monophyllus* **subgen.n.** tergalii II–VII are unilamellate (Figs 121–126). Tergalius I has different structure, often thread-like [see Choroterpes/fg1 (1)].

(3) Each penis lobe has an apical projection dorsad of gonopore; this projection stretches in distal direction and bears fine colorless denticles. Size of this apical projection varies from very small (e.g., in *petersi* Tong et Dudgeon, 2003 [*Choroterpes*]) to very long (Figs 68, 69, 117); its shape varies from rounded (Figs 38, 53, 89) to pointed (Figs 19, 68).

Distribution. Mainly Arctogea (Ethiopian, Oriental, Palaearctic and Nearctic Regions) with a few species in the north of Neotropical Region.

Discussion. During a long time this taxon was confused with *Thraulus* (see above). Eaton, who described both genera — *Choroterpes* and *Thraulus*, distinguished their adults by gonostylus structure: in *Thraulus* gonostylus has 3 segments (1st segment by far the longest, 2nd and 3rd segments short), while for *Choroterpes* he reported 4 segments: 1st segment short and ring-like, 2nd segment by far the longest (corresponds to 1st segment of *Thraulus*), 3rd and 4th segments short (correspond to 2nd and 3rd segments of *Thraulus*) [Eaton, 1881, 1883–1888]. Originally, the genus *Choroterpes* included a single species *Choroterpes lusitanica* Eaton, 1881, which later [Eaton, 1883–1888] was synonymized with *Choroterpes picteti* (Eaton, 1871 [*Leptophlebia*]). Originally, the name *Leptophlebia picteti* was introduced for "*Potamanthus marginatus* Linné" sensu Pictet, 1843–1845 to distinguish it from *Leptophlebia marginata* (Linnaeus, 1767). Eaton did not see the type specimens and translated description of his *Choroterpes picteti* from the Pictet's description of *Potamantus marginatus*. The specimens, on which this description was based, are lost [Kimmins, 1960]. Thus, description of genitals of *Choroterpes* was based on the type specimens of *Choroterpes lusitanica* only. Genitals of this species are figured under the name "*Choroterpes Picteti*" [Eaton, 1883–1888: Pl.12, Fig. 19]; on this figure gonostyli are shown as distinctly 4-segmented, with a ring-like 1st segment. Lectotype of *Choroterpes lusitanica* was figured by Kimmins [1960: Fig. 45]; on this figure gonostyli are shown as 3-segmented, i.e. without separated proximal ring-like "1st segment"; this agrees with specimens from Spain examined by me. Gonostylus of Ephemeroptera consists of 4 muscleless secondary segments (which are not homologous to any limb segments of other arthropods); 1st segment is often thicker than 2nd segment; in leptophlebiids, as well as in most other Ephemeroptera, 1st and 2nd segments are fused together without any suture between them, and can be distinguished one from another only by their thickness; 3rd and 4th segments are separated by sutures and have some passive mobility. In *Choroterpes picteti* (= *Ch. lusitanica*) the 1st segment has a transverse impression on lateral side only (Fig. 19), and Eaton wrongly figured this impression as an integral ring-like suture separating the "segments". So, actually *Choroterpes* and *Thraulus* have no difference in number of segments of gonostyli: in both taxa gonostyli are 4-segmented with 1st and 2nd segments synsclerotic, so that only 3 segments are movably articulated. Because of this confusion some species of Choroterpes/fg2 were originally placed to *Thraulus*; the genera *Euthraulus* Barnard, 1932, *Choroterpides* Ulmer, 1939 and *Thraululus* Ulmer, 1939 were originally described as related to Thraulus, as having 3-segmented gonostyli [Barnard, 1932; Ulmer, 1939], while actually they belong to Choroterpes/fg2.

Peters and Edmunds [1964, 1970] suggested that the taxa *Choroterpes* s.str. and *Euthraulus* could be separated by furcation of MA (distad the middle of MA in *Choroterpes* s.str. and at the middle of MA in *Euthraulus*), furcation of MP (symmetrical in *Choroterpes* s.str. and asymmetrical in *Euthraulus*) and shape of costal projection (symmetrically smooth in *Choroterpes* s.str. and inclined distally in *Euthraulus*). Actually, no one of these characters agrees with *Choroterpes* s.str. and *Euthraulus* determined by larval characters. The species of *Choroterpes* examined by me, have furcation of MA at the middle and furcation of MP asymmetric (Fig. 15). Shape of costal projection of hind wing highly varies among species, both in *Choroterpes* s.str. (Figs 16, 40, 50) and *Euthraulus* (Figs 88, 106).

Bauernfeind [1998] suggested that *Choroterpes* s.str. and *Euthraulus* could be separated by shape of median part of styliger, which is concave in *Choroterpes* s.str. and convex in *Euthraulus*. However, in *Choroterpes* (*Euthraulus*) *signatus* (Hagen, 1858) styliger varies individually from convex (Fig. 111) to concave (Fig. 115).

Demoulin [1981] keyed larvae of African genus *Fulletomimus* Demoulin, 1956 as differing from *Choroterpes* s.l. by a single character — "segments abdominaux à paratergites se terminant par des épines ... doubles (VIII–IX)". However, the same character is found in *Choroterpes* (*Euthraulus*) *signatus* (Hagen, 1858) (Figs 108–109), which has no serrate outer margin of fore wing, characteristic for *Fulletomimus*. Thus, larva ascribed to *Fulletomimus*, can belong to Choroterpes/fg2-Euthraulus/g2.

Classification. The taxon Choroterpes/fg2 is divided into Choroterpes/fg3 and Euthraulus/g1.

1.1.1.1.1. **Choroterpes/fg3**
Figs 2–67

Systematic position: Choroterpes/fg1—Choroterpes/fg2—Choroterpes/fg3.

Hierarchical typified name: Choroterpes/fg3 (sine *Euthraulus*; incl. *Neochoroterpes* Allen, 1974).

Possible ranking names:
— genus *Choroterpes*;
— subgenus *Choroterpes*.

Autapomorphy.

(1) Middle process of tergalius [one of three apical processes of each two lamella — see Choroterpes/fg2 (2)] is narrow at base and lanceolately widened at middle. This feature can be expressed either on both lamellae (Fig. 67), or on dorsal lamella only (Figs 7–12, 31–36, 58–63); rarely not expressed at all (e.g., in *Choroterpes* (*Neochoroterpes*) *kossi* Allen, 1974 and *Ch.* (*N.*) *crocatus* Allen, 1974).

Plesiomorphy. Unlike Euthraulus/g1, penial arms are not strongly arched and not deeply inserted under the ninth abdominal segment (Figs 19, 38, 53, 65).

Classification. The taxon Choroterpes/fg3 is divided into plesiomorphon Choroterpes/fg4 and holophyletic taxon *Neochoroterpes*.

1.1.1.1.1.1. Plesiomorphon **Choroterpes/fg4**
Figs 2–63

Systematic position: Choroterpes/fg1—Choroterpes/fg2—Choroterpes/fg3—pm.Choroterpes/fg4.

Hierarchical typified name: Choroterpes/fg4 (sine *Neochoroterpes*).

Possible ranking names:
— genus *Choroterpes*;
— subgenus *Choroterpes*.

Plesiomorphy. Labrum retains 2 transverse rows of setae — distal and proximal ones (characteristic for Atalophlebopectinata). The transverse setal row can be either regular (Fig. 43), or irregular (Fig. 28), or represent a stripe of irregularly situated setae (Fig. 13).

Distribution and species composition. Distributed mainly in Arctogea (Ethiopian, Oriental, Palaearctic and Nearctic Regions), with a few species in the north of Neo-

tropical Region. The following described species belong here for certain: In Europe: *Ch. picteti picteti* (Eaton, 1871 [*Leptophlebia*]) (= *Ch. lusitanica* Eaton, 1881); *Ch. picteti subcostalis* **ssp.n.**; *Ch. borbonica* Belfiore, 1988; *Ch. prati* Puig et Gaino, 1996; *Ch. salamannai* Gaino et Puig, 1996. In Arabia: *Ch. pacis* Sartori, 1991 and *Ch. ludmilae* **sp.n.**. In northern Africa: *Ch. atlas* Soldán et Thomas, 1983. In South Africa: *Ch. nigrescens* Barnard, 1932 and *Ch. ndebele* Agnew, 1962. In Hong Kong: *Ch. petersi* Tong et Dudgeon, 2003. In Sumatra: *Ch. proba* Ulmer, 1939. In Sulawesi: *Ch. mercatorius* **sp.n.** In North America: *Ch. basalis* (Banks, 1900 [*Leptophlebia*]) (= *Ch. ferruginea* Traver, 1934, = *Ch. fusca* Spieth, 1938, = *Ch. hubbelli* Berner, 1946); *Ch. inornata* Eaton, 1892 (= *Ch. oaxacaensis* Brusca et Allen, 1973); *Ch. albiannulata* McDunnough, 1924; *Ch. terratoma* Seemann, 1927; *Ch. ungulus* Lugo-Ortiz et McCafferty, 1996. In Central America: *Ch. gregoryi* Ávila et Flowers, 2006 and *Ch. mairena* Ávila et Flowers, 2006. Besides this, to *Choroterpes* s.str. are attributed some species described from Europe, Asia and Africa, whose larvae are unknown and systematic position is uncertain. Species examined are reviewed below.

1.1.1.1.1.1-1. Choroterpes/fg4 ***picteti*** [***Choroterpes***] Figs 2–23

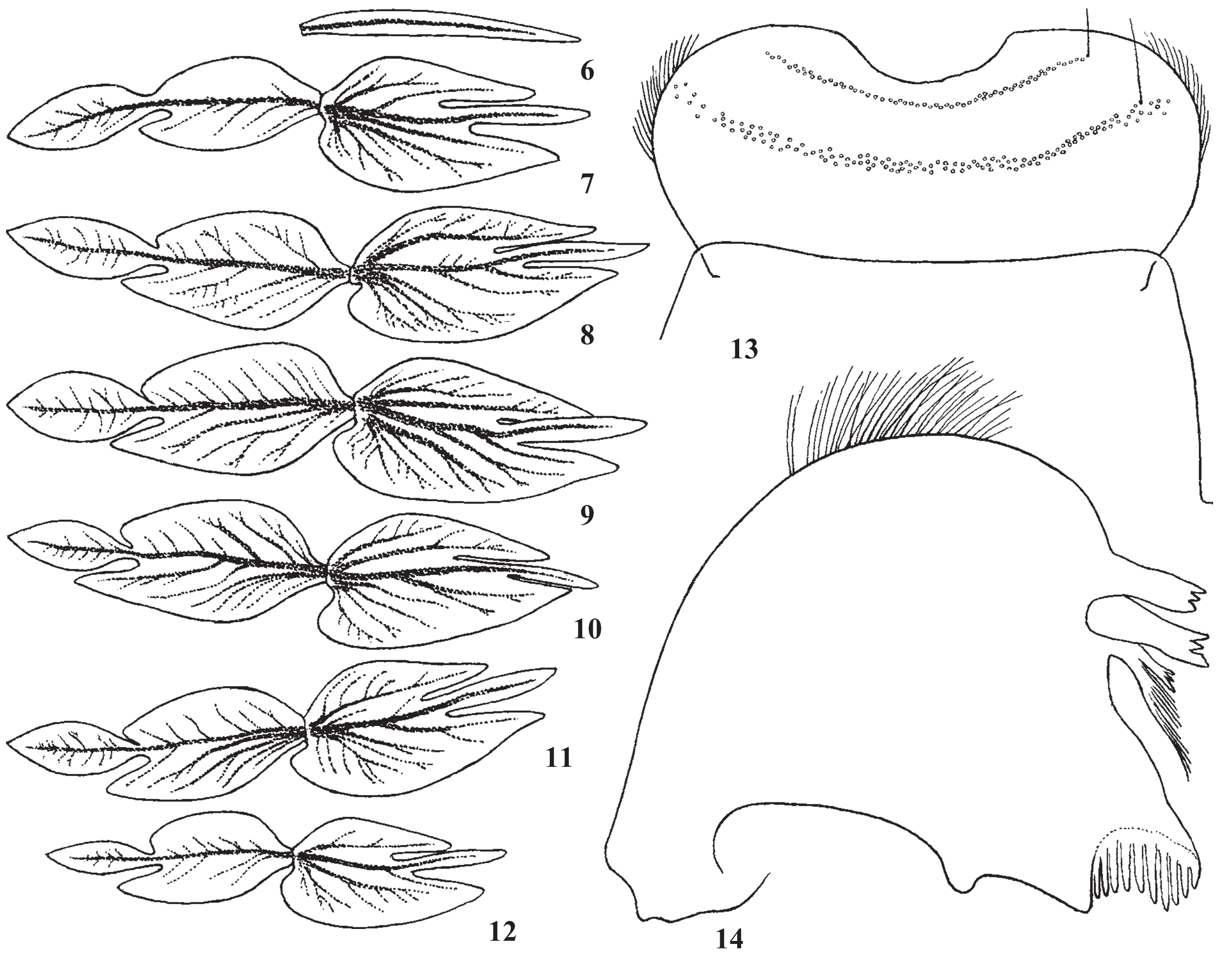
Original binomen: *Choroterpes picteti* Eaton, 1871.
Possible binomina:
— *Choroterpes picteti*;
— *Choroterpes* (*Choroterpes*) *picteti*.

Larva. Adequately described and illustrated in literature [e.g., Eaton, 1883–1888 (Pl.34); Grandi, 1941].

Cuticular coloration: Cuticle nearly colorless, uniformly pale ocher.

Hypodermal coloration: Head and thorax can have dark brown hypodermal markings; abdomen can have dark brown hypodermal markings as in imago.

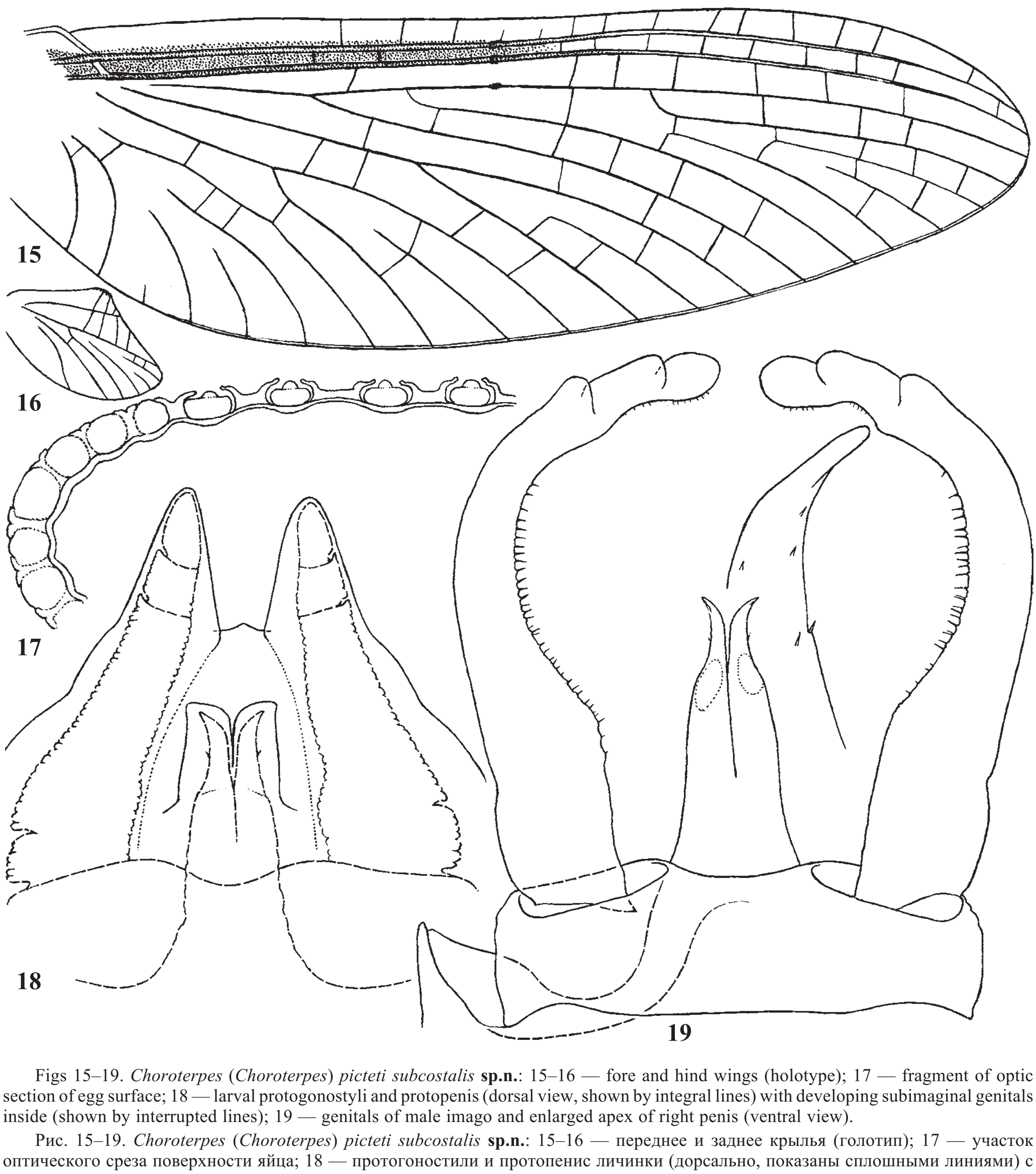
Shape and setation: Labrum has median emargination very wide, with angulate margins; distal transverse setal row somewhat irregular; proximal transverse setal row wide and irregular (Fig. 13). Mandibles with outer margin very convex (Fig. 14). Medio-apical projection of maxilla differently expressed in two subspecies (Figs 4–5). Femur of fore leg has the same width proximally and at middle, femora of middle and hind legs widest at middle. Stout setae on outer side of femora blunt and pointed,



Figs 6–14. *Choroterpes* (*Choroterpes*) *picteti subcostalis* **sp.n.**, larva: 6–12 — tergalii I–VII (dorsal lamella bent to the left); 13 — labrum; dorsal view (instead of setae of distal and proximal transverse rows, only their bases are shown); 14 — left mandible; 6–13 — holotype.

Рис. 6–14. *Choroterpes* (*Choroterpes*) *picteti subcostalis* **sp.n.**, larva: 6–12 — I–VII тергалии (дорсальный листок отогнут влево); 13 — верхняя губа, дорсально (вместо щетинок дистального и проксимального поперечных рядов показаны только их основания); 14 — левая мандибула; 6–13 — голотип.

short and long, located irregularly. Pectinate setae on ventral side of hind femur pointed and curved, form a stripe parallel to inner margin of femur (similar to Figs 150, 151). Stout setae on inner side of fore tibia situated densely and irregularly; each seta pointed, with two rows of stout pointed processes by sides. Middle tibia with very short sparse stout setae irregularly located on inner side only. Hind tibia with sparse stout bipectinate setae, irregularly located on all sides; outer side of hind tibia with blunt setae of variable length, as on outer side of femur [Grandi, 1941: Fig. IX.1, 3, 4]. Outer sides of all tibiae with irregularly situated thin hairs, whose length exceed tibia width. Abdomen without stout setae. Posterolateral spines expressed beginning from abdominal segment II or III. Abdominal tergum I with vestigial denticles on hind margin; terga II–X and segments of caudalii with long pointed denticles on hind margins. Tergalii II–VII [see Choroterpes/fg3 (1)] have all processes developed, except for costal process of dorsal lamella of tergalius II, which can be absent (Figs 7–12). Protopenes of mature male larva short, pressed together, with apices pointed and divergent, completely hidden under sternum XI (Fig. 18). Female larva has hind margin of abdominal sternum IX rounded, without any incision [Grandi, 1941: Fig. X.2].



Figs 15–19. *Choroterpes* (*Choroterpes*) *picteti subcostalis* **sp.n.**: 15–16 — fore and hind wings (holotype); 17 — fragment of optic section of egg surface; 18 — larval protogonostyli and protopenis (dorsal view, shown by integral lines) with developing subimaginal genitals inside (shown by interrupted lines); 19 — genitals of male imago and enlarged apex of right penis (ventral view).

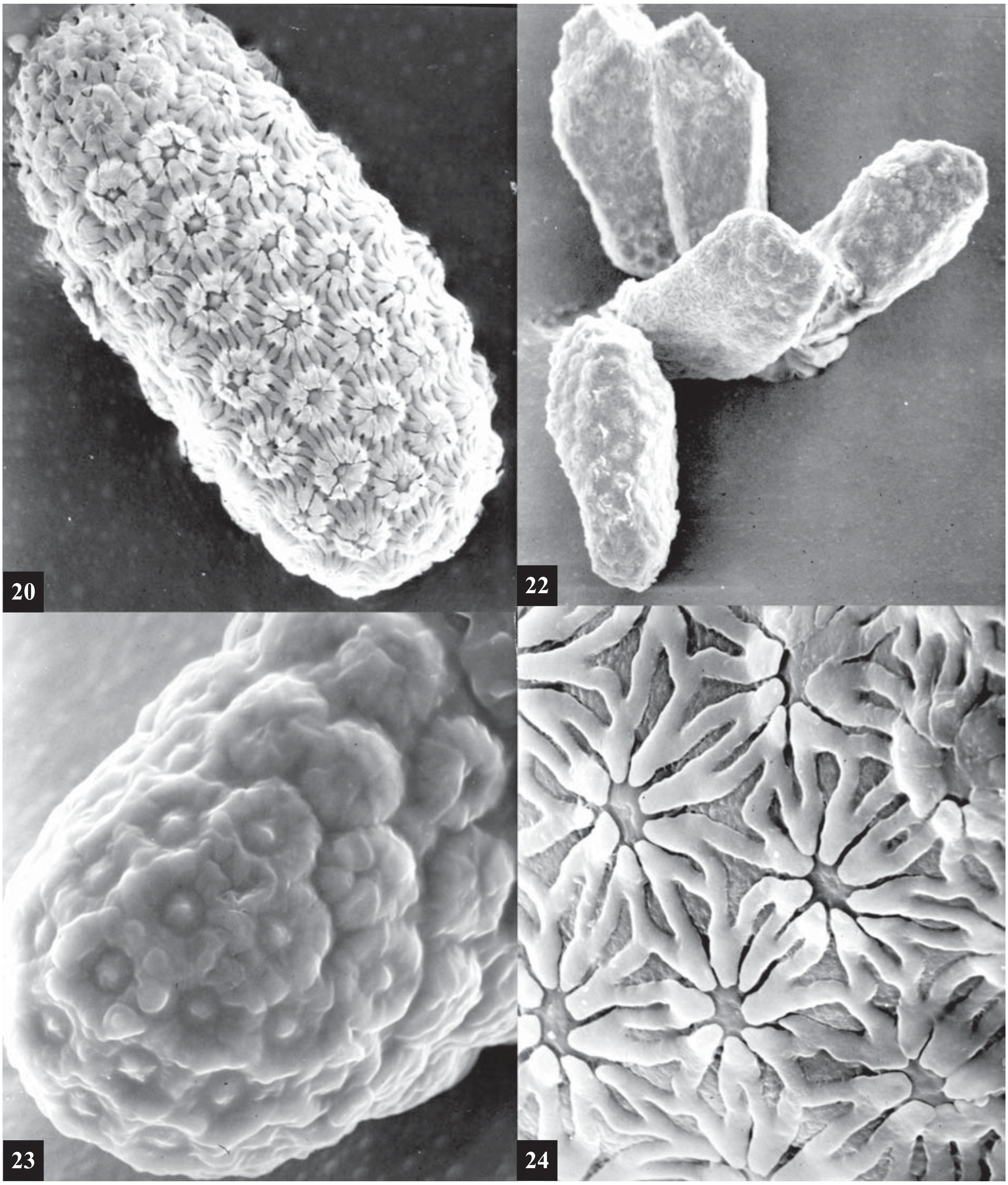
Рис. 15–19. *Choroterpes* (*Choroterpes*) *picteti subcostalis* **sp.n.**: 15–16 — переднее и заднее крылья (голотип); 17 — участок оптического среза поверхности яйца; 18 — протогоностили и протопенис личинки (дорсально, показаны сплошными линиями) с развивающимися субимагинальными гениталиями внутри (показаны прерывистыми линиями); 19 — гениталии самца имаго и увеличенный правый пенис (вентрально).

Subimago. Cuticular coloration: Cuticle of thorax at most light; furcasternal protuberances brownish; mesonotum at most brown; most part of medioscutum and submedioscutum brown, posterior scutal protuberance brown except median part (as in Fig. 92). Cuticle of legs light brownish. Wings light brownish. Cuticle of abdomen light brownish, cuticle of gonostyli brown.

Hypodermal coloration: Abdomen with brown maculae as in imago.

Texture: Tarsus of each leg covered by microtrichiae of the same shape as microtrichiae on tibia; only on distal part of 5th tarsomere microtrichiae are gradually substituted by pointed microlepides.

Imago, male. Adequately described and illustrated in literature [e.g., Grandi, 1941]. Head dark brown; dorsal eyes not elevated, brownish-orange. Thorax brown, with membranes ocher. On fore wing at least subcostal area colored with brown in proximal half (in *Ch. p. subcostalis* — Fig. 15),



Figs 20–23. *Choroterpes* (*Choroterpes*) *picteti*, eggs: 20 — *Ch.* (*Ch.*) *picteti picteti*; 21–23 — *Ch.* (*Ch.*) *picteti subcostalis* **sp.n.**
Рис. 20–23. *Choroterpes* (*Choroterpes*) *picteti*, яйца: 20 — *Ch.* (*Ch.*) *picteti picteti*; 21–23 — *Ch.* (*Ch.*) *picteti subcostalis* **sp.n.**

or both costal and subcostal areas colored with brown (in. *Ch. p. picteti*); pterostigma with about 10 nearly transverse simple crossveins. Hind wing with costal projection blunt (Fig. 16). Femur of each leg brown, darkened at apex; tibia lighter brownish, darkened at base. Abdomen ocher-brownish, each tergum with a pair of large diffusive hypodermal brown maculae widened posteriorly [Grandi, 1941: Fig. XI]. Styliger, gonostyli and penis brown. 1st+2nd segments of gonostylus with inner margin angulate. Each penis has apical projection [see Choroterpes/fg2 (3)] pointed and bent laterally-ventrally; its denticles are few and small (Fig. 19). Caudalii uniformly brown.

Imago, female. Adequately described and illustrated in literature [e.g., Grandi, 1941]. Coloration as in male. Posterior plate of abdominal sternum IX apically rounded, without incision [Grandi, 1941: Fig. XIX.3].

Egg. Brownish-yellow; relatively narrow, cylindrical. Chorion bears evenly dispersed papillae and ridges going from one papilla to another [see Choroterpes/fg2 (1)]; papillae high, so that each papilla surrounded by overlapping ridge angles, represents a prominent protuberance; in *Ch. picteti picteti* this relief is the same on the whole egg surface (Fig. 20); in *Ch. p. subcostalis* **ssp.n.** one pole differs from the rest surface (Figs 17, 21–23).

DIMENSION. Fore wing length 8 mm.

COMPOSITION. *Choroterpes picteti* is represented by two subspecies — *Ch. picteti picteti* and *Ch. picteti subcostalis* **ssp.n.**

1.1.1.1.1.1-1.1. Choroterpes/fg4 ***picteti picteti*** [***Choroterpes***] Figs 5, 20

Original binomen: *Choroterpes picteti* Eaton, 1871.
Possible binomina:
— *Choroterpes picteti picteti*;
— *Choroterpes* (*Choroterpes*) *picteti pictetri*.

MATERIAL. Imagoes and larvae from Spain, Switzerland, Czech Republic and western Ukraine. River Teterev near Zhitomir, 8.VIII.1928: 7 larvae.

Larva. Adequately described and illustrated in literature [e.g., Eaton, 1883–1888: Pl.34; Grandi, 1941]. Medio-apical projection of maxilla not large, less than 1/2 of dentiseta length (Fig. 5).

Imago. Adequately described and illustrated in literature [e.g., Grandi, 1941; Bauernfeind, 1998].

Wing colotration. On fore wing both costal and subcostal fields entirely colored with brown [Eaton, 1883–1888: Pl. 12, Fig.19; Grandi, 1941: Fig. XI].

Egg. Adequately described and illustrated in literature [Grandi, 1941; Gaino & Puig, 1996; Haybach, 2003]. Relief characteristic for *Ch. picteti* (see above) is the same on all parts of egg (Fig. 20).

DISTRIBUTION. Europe to the east up to Zhitomir Region of Ukraine.

1.1.1.1.1.1-1.2. Choroterpes/fg4 ***picteti subcostalis*** **ssp.n.** [***Choroterpes***] Figs 2–4, 6–19, 21–23

Original binomen: *Choroterpes* (*Choroterpes*) *picteti subcostalis* Kluge, **ssp.n.**

MATERIAL. Holotype: L-S-I♂ {specimen [XIX](7)85}: RUSSIA, Krasnodar Territory, river Psekups near railway station Goryachiy Kluch, 27.VIII.1985, coll. N. Kluge. Paratypes: the same locality, 26–28.VIII.1985: 5 L-S-I♂, 2 L-S♀, 1 I♂, 20 larvae; river Psekups near railway station Fanogoriyskaya, 25–27.VIII.1991, coll. N. Kluge: 1 L-S♂, 1 S♂, 3 larvae; river Il', X.1979, coll. E. Kryuchkova: 35 larvae.

Larva. Medio-apical projection of maxilla large, exceeds 1/2 of dentiseta length (Fig. 4).

Imago. Wing colotration. On fore wing only proximal part of subcostal field colored with brown; costal field nearly colorless (Fig. 15). This coloration is expressed only in imago, but not in subimago and larva: subimaginal fore wing entirely gray; larval fore protopteron either colorless, or with longitudinal brown hypodermal stripe at base of subcostal field; this stripe is not so long as the colored area of imago.

Egg. Chorion with relief characteristic for *Ch. picteti* (see above); on one pole papillae are enlarged and brought together (Figs 17, 21–23).

DISTRIBUTION. Known only from western Caucasus.

COMPARISON. *Ch.* (*Ch.*) *picteti subcostalis* **ssp.n.** differs from *Ch. p. picteti* by size of medio-apical projection of larval maxilla, by coloration of imaginal fore wing and by chorion structure of egg.

1.1.1.1.1.1-2. Choroterpes/fg4 ***nigrescens*** [***Choroterpes***]

Original binomen: *Choroterpes nigrescens* Barnard, 1932.
Possible binomina:
— *Choroterpes nigrescens*;
— *Choroterpes* (*Choroterpes*) *nigrescens*.

REFERENCES: Barnard, 1984: imago and larva; Agnew, 1962: comparison of imago and larva.

MATERIAL. South Africa, Berg river, western Cape, 09.II.1994, coll. F.C. de Moor: 1 male larva.

DISTRIBUTION. South Africa.

1.1.1.1.1.1-3. Choroterpes/fg4 ***ludmilae*** **sp.n.** [***Choroterpes***] Figs 24–42

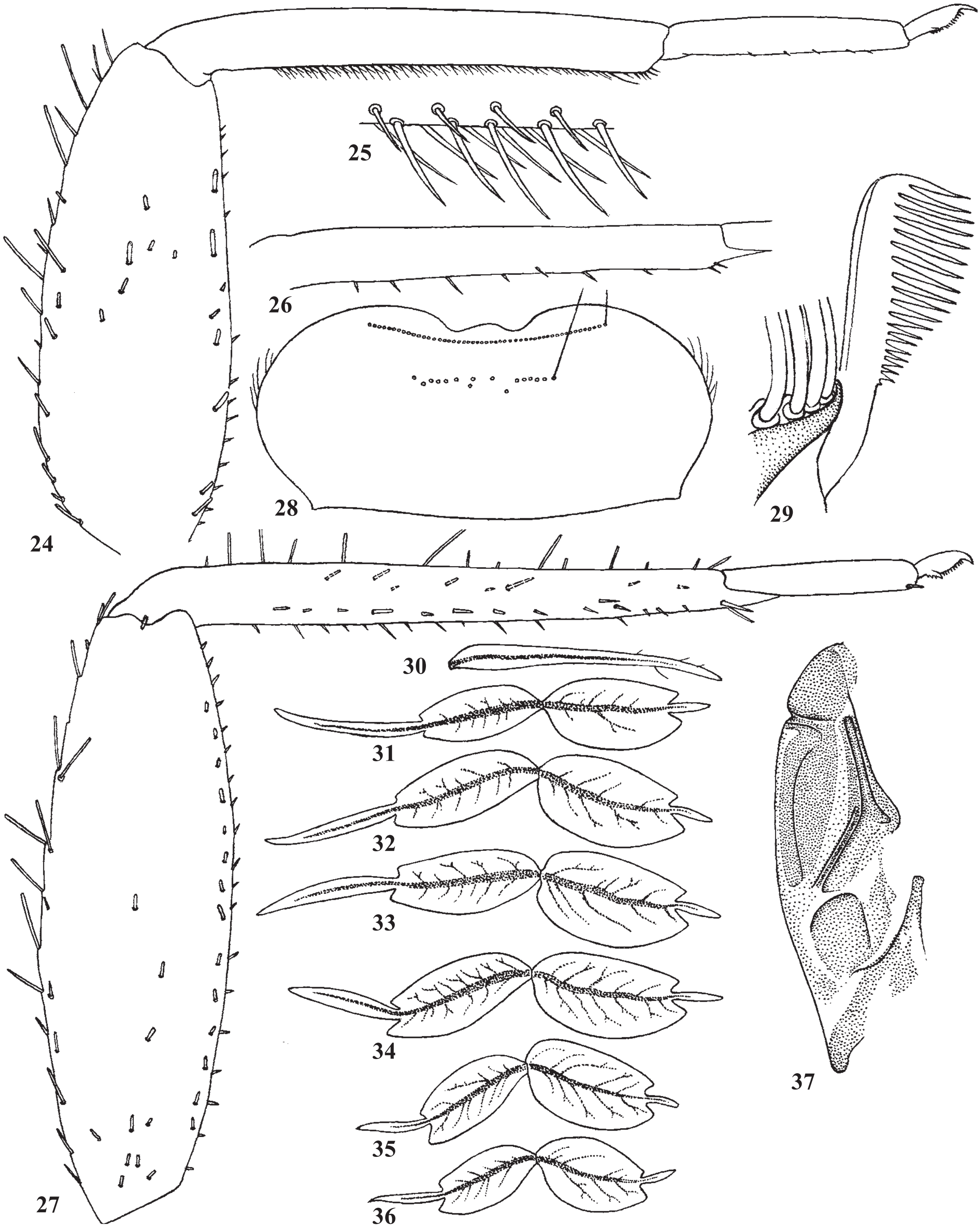
Original binomen: *Choroterpes* (*Choroterpes*) *ludmilae* **sp.n.**

MATERIAL. Holotype: L-S-I# {specimen [I](1)2010}: OMAN, Hatta Pools, 28.X.2010, coll. Ludmila Sheyko. Paratypes: the same locality, 2 L/S#, 1L/S$, 32 larvae.

Larva. Cuticular coloration: Head, labrum and exposed parts of mandibles brown; each mandible with roundish diffusive blank. Pronotum brown, with lateral margins colorless. Mesonotum brown. Thoracic pleura partly brown, sterna light. Cuticle of femora with diffusive brown and light areas; tibiae and tarsi brown. Abdomen has terga brown; sterna light, with diffusive brown markings by sides and on styliger. Caudalii brown.

Hypodermal coloration: Head and thorax can have dark brown hypodermal maculation; abdomen and legs with brown maculation as in imago.

Shape and setation: Labrum has median emargination shallow, with convexity in middle; distal transverse setal row regular; proximal transverse setal row small and regular or nearly regular (Fig. 28). Mandibles with outer margin moderately convex (similar to Fig. 44). Medio-apical projection of maxilla poorly expressed (Fig. 29). Femur of fore leg widest at proximal part (Fig. 24), femora of middle and hind legs widest at middle (Fig. 27). Stout setae on outer side of femora blunt, vary from short to very long, located irregularly. Pectinate setae on ventral side of hind femur small and ovoid, form a single irregular row parallel to inner margin of femur (Fig. 27). Stout setae on inner side of fore tibia dense and arranged in 3 nearly regular rows (Fig. 25); side processes of these setae either thin and short, or absent. Middle tibia with sparse stout setae irregularly located on inner side only (Fig. 26). Hind tibia with sparse stout non-pectinate setae of variable length, irregularly located on all sides; outer side of hind tibia with blunt setae of variable length, as on outer side of femur. Outer sides



Figs 24–37. *Choroterpes* (*Choroterpes*) *ludmilae* **sp.n.**: 24–36 — larva: 24 — fore leg (dorsal view); 25 — setae on inner side of fore tibia; 26 — tibia of middle leg; 27 — hind leg (dorsal view); 28 — labrum, dorsal view (instead of setae of distal and proximal transverse rows, only their bases are shown); 29 — medio-apical projection of maxilla, ventral view (dotted); 30–36 — tergalii I–VII (dorsal lamella bent to the left); 37 — exuviae of right half of subimaginal mesonotum; 24–27, 30–37 — holotype.

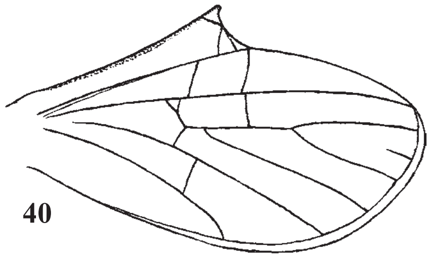
Рис. 24–37. *Choroterpes* (*Choroterpes*) *ludmilae* **sp.n.**: 24–36 — личинка: 24 — передняя нога (дорсально); 25 — щетинки на внутренней стороне передней голени; 26 — голень средней ноги; 27 — задняя нога (дорсально); 28 — верхняя губа, дорсально (вместо щетинок дистального и проксимального поперечных рядов показаны только их основания); 29 — медио-апикальный выступ максиллы, вентрально (пунктирован); 30–36 — I–VII тергалии (дорсальный листок отогнут влево); 37 — экзувий правой половины субимагинального мезонотума; 24–27, 30–37 — голотип.



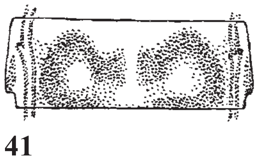
38



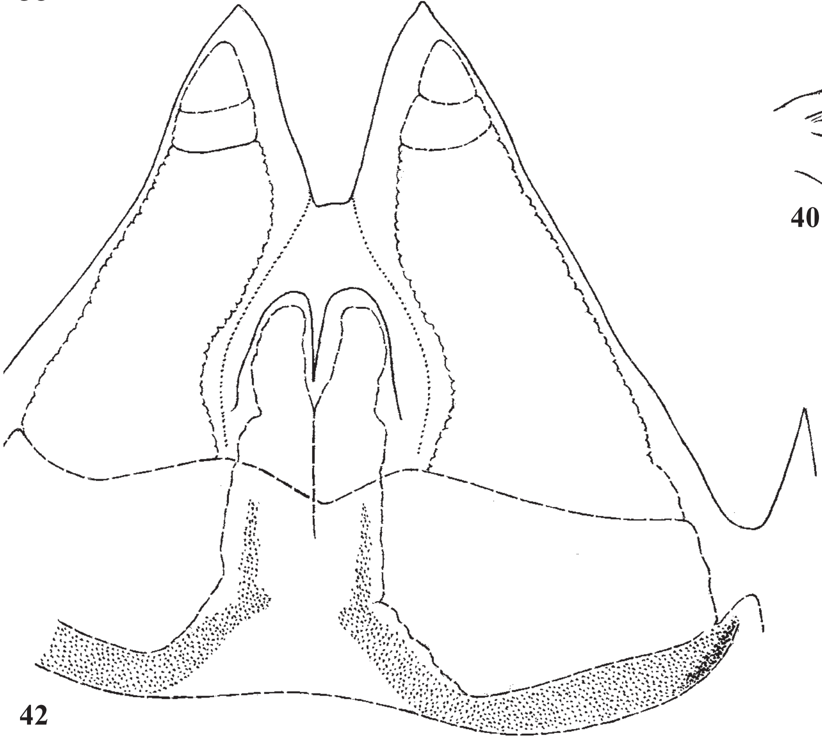
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40



41



42

Figs 38–42. *Choroterpes* (*Choroterpes*) *ludmilae* **sp.n.**: 38 — genitals of male imago, ventral view; 39 — gonostylus of subimago; 40 — hind wing; 41 — tergum VI of abdomen of male imago; 42 — larval protogonostyli and protopenis (dorsal view, shown by integral lines) with developing subimaginal genitals inside (shown by interrupted lines); 38–41 — holotype.

Рис. 38–42. *Choroterpes* (*Choroterpes*) *ludmilae* **sp.n.**: 38 — гениталии самца имаго, вентрально; 39 — гоностиль субимаго; 40 — заднее крыло; 41 — VI тергит брюшка самца имаго; 42 — протогоностили и протопенис личинки (дорсально, показаны сплошными линиями) с развивающимися субимагинальными гениталиями внутри (показаны прерывистыми линиями); 38–41 — голотип.

of all tibiae with irregularly situated thin hairs, whose length exceed tibia width (not shown in Figs 24–27). Abdomen without stout setae. Posterolateral spines expressed beginning from abdominal segment V or VI. Abdominal tergum I with vestigial denticles on hind margin; terga II–IX with small triangular denticles — either equilateral or longer; tergum X and each segment of caudalii with longer denticles; sterna without denticles. Tergalii II–VII [see Choroterpes/fg3 (1)] have simplified structure: ventral lamella has side processes very short, median process diminished; dorsal lamella has side processes extremely short, median process narrow (Figs 31–36). Protogonostyli of male larva nearly contiguous at base; protopenes short, divergent, completely hidden under sternum XI (Fig. 42). Female larva has hind margin of abdominal sternum IX deeply incised (as in Fig. 54).

Subimago. Cuticular coloration: Cuticle of thorax at most light, mesonotum at most brown: most part of medioscutum and submedioscutum brown, posterior scutal protuberance brown except median part (Fig. 37). Cuticle of legs colorless. Wings light brownish. Cuticle of abdomen colorless, cuticle of gonostyli brown.

Hypodermal coloration: Legs and abdomen with brown maculation as in imago.

Texture: On each leg 1st tarsomere (shortened and fused with tibia) covered by microtrichiae of the same shape as microtrichiae on tibia; 2nd–5th tarsomeres covered by pointed microlepides.

Imago, male. Head dark brown; dorsal eyes not elevated [as in Kluge, 1984: Fig. 22], brownish-orange. Thorax dark brown, with membranes whitish. On fore wing basal sclerites brownish, veins and membrane colorless; pterostigma whitish, with 6–7 simple oblique crossveins. Hind wing with costal process stretched, pointed and inclined distally (Fig. 40). Femur of each leg light, with dark brown hypodermal macula near apex and diffusive hypodermal macula at middle; on middle and hind legs this middle macula is nearly absent. Tibia of each leg at most colorless, with light brown cuticular pigment at base. Abdominal terga II–IX with repeated dark brown hypodermal ornament on colorless background (Fig. 41); sterna colorless. Gonostyli colorless, penis light brownish. 1st+2nd segments of gonostylus with inner margin non-angulate. Each penis has apical projection [see Choroterpes/fg2 (3)] not long, bent medially, with apex roundish; its denticles are small, directed distally (Fig. 38). Caudalii light, at proximal part of each caudalius, articulations of segments with contrasting hypodermal dark brown coloration.

Imago, female. Unknown.

Egg. Unknown.

DIMENSION. Fore wing length 4 mm.

DISTRIBUTION. Known from a single point in Oman.

COMPARISON. *Ch. ludmilae* **sp.n.** is similar to *Ch. pacis* Sartori, 1991, which was originally described as male imagoes from Oman [Sartori, 1991] and redescribed by Gattolliat & Sartori (2008) based on larvae and subimagoes collected in United Arab Emirats and presumably attributed to this specie. Imago of *Ch. ludmilae* **sp.n.** differs from *Ch. pacis* by sharp costal projection of hind wing, coloration of male imaginal abdomen and absence of dark longitudinal stripes on legs. Among *Choroterpes* s.str., besides *Ch. ludmilae* **sp.n.**, sharp costal projection occurs in *Ch. petersi* Tong & Dudgeon, 2003 and *Ch. mercatorius* **sp.n.**; both species differ from *Ch. ludmilae* **sp.n.** by angulate inner margin of gonostyli and different shape of penis.

ETYMOLOGY. The species is named in honor of Ludmila Sheyko, my wife, who is the first to rear mayfly imago from larva in Arabian Peninsula.

1.1.1.1.1.1-4. Choroterpes/fg4 *mercatorius* sp.n. [*Choroterpes*] Figs 43–63

Original binomen: *Choroterpes* (*Choroterpes*) *mercatorius* **sp.n.**

MATERIAL. Holotype: L-S-I♂ {specimen [XXI](7)}: INDONESIA, Sulawesi Island, Pinrang 31.VIII.2009, coll. N. Kluge & L. Sheyko. Paratypes: the same locality, 28–31.VIII.2009: 1 L-S-I♀, 2 L-S♂, 1 L-S♀, 1 S-I♂, 1 S♀, 7 larvae.

Larva. Cuticular coloration: Cuticle of head, thorax, legs and abdomen either colorless, or with diffusive light brownish markings.

Hypodermal coloration: Head and thorax can have dark brown hypodermal maculation; abdomen with brown maculation as in imago.

Shape and setation: Labrum has median emargination shallow, with vestigial blunt denticles; distal transverse setal row regular; proximal transverse setal row small and regular (Fig. 43). Mandibles with outer margin moderately convex (Fig. 44). Medio-apical projection of maxilla poorly expressed (as in Fig. 29). Femur of fore leg has the same width proximally and at middle (Fig. 46), femora of middle and hind legs widest at middle (similar to Fig. 27). Femora with irregularly situated stout setae of various length and shape — blunt and pointed, pectinate and smooth. Pectinate setae on ventral side of hind femur pointed and curved, form a stripe parallel to inner margin of femur (similar to Figs 150–151). Stout setae on inner side of fore tibia situated densely and irregularly, bipectinate (pointed, with two rows of stout pointed processes by sides). Inner side of middle tibia with a row of stout setae, which are longer than setae on inner sides of fore and hind tibiae (Fig. 47). Hind tibia with sparse stout bipectinate and non-bipectinate setae, irregularly located on all sides; outer side of hind tibia with stout setae of variable length, as on outer side of femur (Fig. 48). Outer sides of all tibiae with irregularly situated thin hairs, whose length exceed tibia width (not shown in Figs 46–48). Each abdominal segment IV–IX with a row of stout blunt setae on each lateral margin (Fig. 55). Posterolateral spines expressed beginning from abdominal segment V. Abdominal tergum I without denticles on hind margin; terga II–IX with small triangular pointed denticles; tergum X and each segment of caudalii with longer denticles; sterna without denticles. Tergalii II–VII [see Choroterpes/fg3 (1)] have costal process of dorsal lamella reduced: on tergalius II it is absent, on tergalii II–VII absent or very small; other processes well developed (Figs 58–63). Protogonostyli of male larva nearly contiguous at base; protopenes very short, convergent, completely hidden under sternum XI (Fig. 55). Female larva has hind margin of abdominal sternum IX deeply incised (Fig. 54).

Subimago. Cuticular coloration: Cuticle of thorax at most light; mesonotum at most light brownish, only sutures (anteronotal transverse impression, anterolateral scutal costa, antelateroparapsidal and lateroparapsidal sutures) darker brown. Cuticle of legs colorless. Wings light brownish. Cuticle of abdomen colorless, cuticle of gonostyli light brownish.

Hypodermal coloration: Abdomen with brown maculation as in imago.

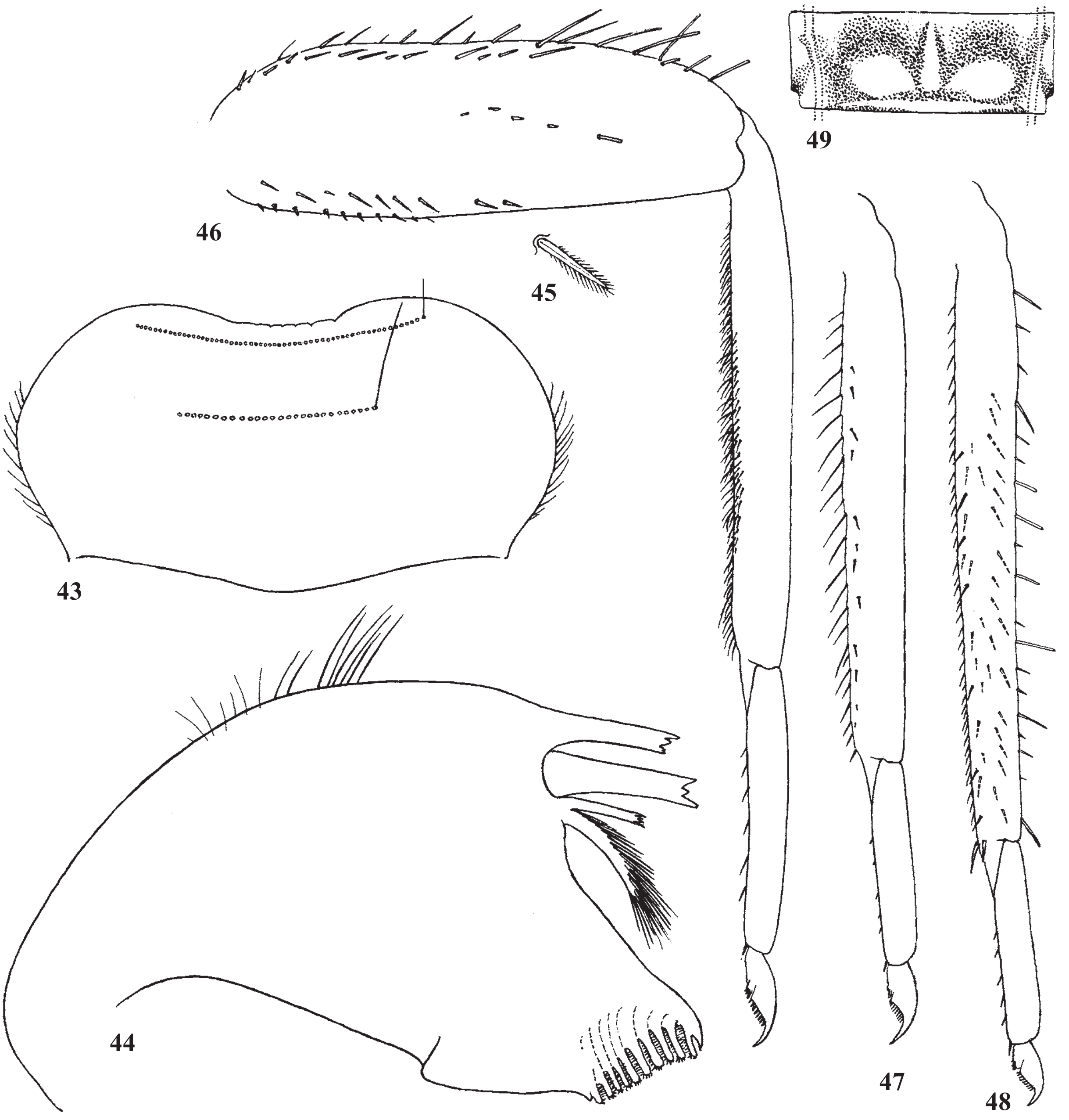
Texture: On each leg 1st tarsomere (shortened and fused with tibia) covered by microtrichiae of the same shape as microtrichiae on tibia; 2nd–5th tarsomeres covered by pointed microlepides.

Imago, male. Head brown; dorsal eyes not elevated [as in Kluge, 1984: Fig.22], brownish-orange. Thorax brown with ocher. On fore wing basal sclerites brownish, veins light, membrane colorless; pterostigma whitish, with 6–8 simple oblique crossveins. Hind wing with costal process stretched, pointed and inclined distally (Fig. 50). Legs light; on each leg

cuticle of knee area (apex of femur and base of tibia) colored by light brown; hypodermal coloration similar to that of female (see below), but poorly developed. Abdominal terga II–IX with repeated dark brown hypodermal ornament on colorless background (Fig. 49); sterna colorless. Gonostyli light brownish, penis lighter. $1^{st}+2^{nd}$ segments of gonostylus with inner margin angulate. Penes short; each penis has apical projection [see Choroterpes/fg2 (3)] not long, bent laterally, with apex roundish; its denticles are well developed and directed distally (Fig. 53). Caudalii light.

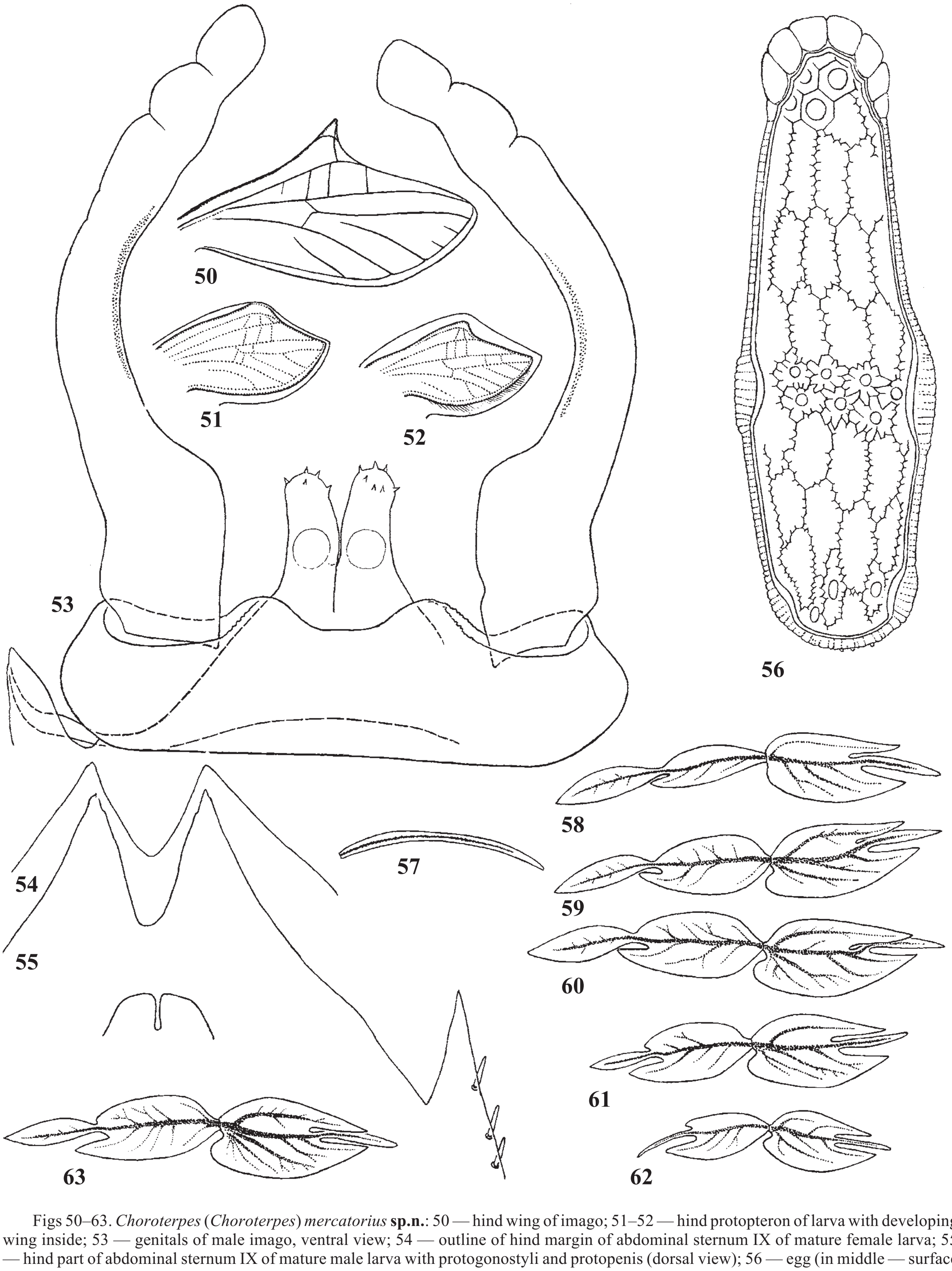
Imago, female. Head and thorax brown with ocher. Legs with cuticular coloration as in male; femora with dark brown hypodermal maculation: band near apex of fore, middle and hind femur and longitudinal stripe at middle of hind femur. Abdomen ocher with brown hypodermal ornament as in male. Posterior plate of abdominal sternum IX apically deeply incised (as in larva — Fig. 54).

Egg. White, without any pigmentation; long and narrow. Chorion has unique relief: papillae surrounded by crowns of broken ridges [see Choroterpes/fg2 (1)] are located only on



Figs 43–49. *Choroterpes* (*Choroterpes*) *mercatorius* **sp.n.**: 43–48 — larva: 43 — labrum, dorsal view (instead of setae of distal and proximal transverse rows, only their bases are shown); 44 — left mandible; 45 — seta on inner side of fore femur; 46 — fore leg (dorsal view); 47 — tibia and tarsus of middle leg; 48 — tibia and tarsus of hind leg; 49 — tergum VI of abdomen of male imago; 45–49 — holotype.

Рис. 43–49. *Choroterpes* (*Choroterpes*) *mercatorius* **sp.n.**: 43–48 — личинка: 43 — верхняя губа, дорсально (вместо щетинок дистального и проксимального поперечных рядов показаны только их основания); 44 — левая мандибула; 45 — щетинка на внутренней стороне переднего бедра; 46 — передняя нога (дорсально); 47 — голень и лапка средней ноги; 48 — голень и лапка задней ноги; 49 — VI тергит брюшка самца имаго; 45–49 — голотип.



Figs 50–63. *Choroterpes* (*Choroterpes*) *mercatorius* **sp.n.**: 50 — hind wing of imago; 51–52 — hind protopteron of larva with developing wing inside; 53 — genitals of male imago, ventral view; 54 — outline of hind margin of abdominal sternum IX of mature female larva; 55 — hind part of abdominal sternum IX of mature male larva with protogonostyli and protopenis (dorsal view); 56 — egg (in middle — surface view, in periphery — optic section); 57–63 — tergalii I–VII (dorsal lamella bent to the left); 50, 53, 57–63 — holotype.

Рис. 50–63. *Choroterpes* (*Choroterpes*) *mercatorius* **sp.n.**: 50 — заднее крыло имаго; 51–52 — задний протоптерон личинки с развивающимся задним крылом внутри; 53 — гениталии самца имаго, вентрально; 54 — очертание заднего края IX стернита брюшка зрелой личинки самки; 55 — задняя часть IX стернита брюшка зрелой личинки самца с протогоностилями и протопенисом (дорсально); 56 — яйцо (в середине — вид поверхности, по периферии — оптический срез); 57–63 — I–VII тергалии (дорсальный листок отогнут влево); 50, 53, 57–63 — голотип.

poles and equator; on one pole papillae are very large and pressed together with ridges; on another pole and on equator papillae have moderate size, each being surrounded by a crown of broken ridges; areas between each pole and equator are filled with crowns of broken ridges stretched in longitudinal direction (Fig. 56).

DIMENSION. Fore wing length 5 mm.

DISTRIBUTION. Sulawesi.

COMPARISON. Among *Choroterpes* s.str., besides *Ch. mercatorius* **sp.n.**, sharp costal projection occurs in *Ch. ludmilae* **sp.n.** and *Ch. petersi* Tong & Dudgeon, 2003; both species differ from *Ch. mercatorius* **sp.n.** by longer penis. Larva differs from other examined species of *Choroterpes* s.l. by the following characters: stout setae on inner side of middle tibia are longer than setae on inner sides of fore and hind tibiae; abdomen with stout setae on lateral margin.

ETYMOLOGY. The species was collected in a street market located on banks of a canal in the town of Pinrang.

1.1.1.1.1.2. **Neochoroterpes/g(1)**, or ***Neochoroterpes*** Figs 64–67

Systematic position: Choroterpes/fg1—Choroterpes/fg2—Choroterpes/fg3—*Neochoroterpes*.

Hierarchical typified name: Neochoroterpes/g1 [g: *Neochoroterpes* Allen, 1974; type species: *Choroterpes* (*Neochoroterpes*) *mexicanus* Allen, 1984].

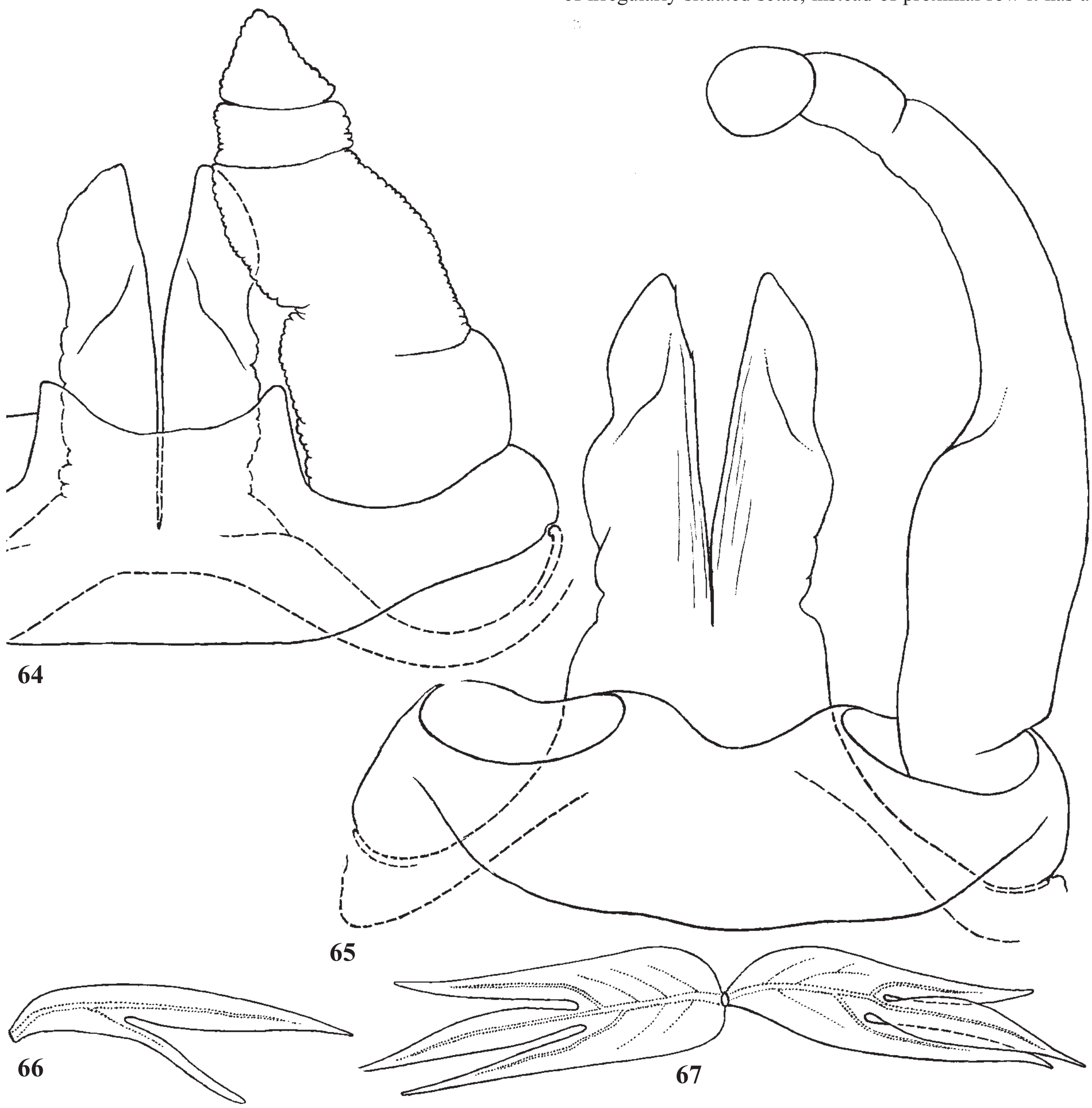
Possible rank-based names:

— genus *Neochoroterpes*;

— subgenus *Neochoroterpes* in genus *Choroterpes*.

Autapomorphy.

(1) Labrum lost transverse setal rows characteristic for Atalophlebopectinata: instead of distal row it has a wide field of irregularly situated setae, instead of proximal row it has a



Figs 64–67. *Choroterpes* (*Neochoroterpes*) *oklahoma*: 64 — crumpled genitals of male subimago, extracted from larva (ventral view); 65 — genitals of male imago (ventral view); 66, 67 — tergalii I and IV.

Рис. 64–67. *Choroterpes* (*Neochoroterpes*) *oklahoma*: 64 — смятые гениталии самца субимаго, отпрепарированные из личинки (вентрально); 65 — гениталии самца имаго (вентрально); 66, 67 — I и IV тергалии.

larger field of irregularly situated longer setae [Henry, 1993: Figs 1–4].

Distribution and species composition. Distributed in New World, mainly in southern part of North America. 6 species are formally described: *nanita* Traver, 1934 [*Choroterpes*], *oklahoma* Traver, 1934 [*Choroterpes*], *mexicanus* Allen, 1974 [*Choroterpes* (*Neochoroterpes*)], *crocatus* Allen, 1974 [*Choroterpes* (*Neochoroterpes*)], *kossi* Allen, 1974 [*Choroterpes* (*Neochoroterpes*)] and *orientalis* Henry, 1993 [*Neochoroterpes*]. Among them, *crocatus* [*Choroterpes*] is regarded to be a junior synonym of *nanita* [*Choroterpes*] [Henry, 1993]. The same author regarded *mexicanus* [*Choroterpes*] to be a junior synonym of *oklahoma* [*Choroterpes*] [Henry, 1993]. However, subimaginal penis of *mexicanus* [*Choroterpes*], figured in the original description [Allen, 1974: Figs 4–5] is very short and triangular, similar to penis of *nanita* [*Choroterpes*] [Traver, 1934: Fig. 2; Henry, 1993: Fig. 25]; in contrast to this, penis of *oklahoma* [*Choroterpes*] is much longer, with widened apices, being the same in imago and subimago (Figs 64–65).

1.1.1.1.1.2-1. Neochoroterpes/g(1) ***oklahoma*** [***Choroterpes***] Figs 64–67

Original binomen: *Choroterpes oklahoma* Traver, 1934.
Possible binomina:
— *Neochoroterpes oklahoma*;
— *Choroterpes* (*Neochoroterpes*) *oklahoma*.
REFERENCES: Traver, 1934: imago; Henry, 1993: imago and larva.
MATERIAL. USA, Texas, Runnels Co., Rd3115, Colorado River, 15.III.1993, B. Kondratieff: 11 I♂, 1 I♀, 1 L/S♂, 2 L/S♀.
DISTRIBUTION. Southern Nearctic.

1.1.1.1.2. **Euthraulus/g1** Figs 68–151

Systematic position: Choroterpes/fg1—Choroterpes/fg2—Euthraulus/g1.
Hierarchical typified name: Euthraulus/g1 (incl. *Monophyllus*, *Dilatognathus*) [g: *Euthraulus* Barnard, 1932; type species: *E. elegans* Barnard, 1932].
Possible rank-based names:
— genus *Euthraulus*;
— subgenus *Euthraulus* in genus *Choroterpes*.

Autapomorphy.
(1) Penial arms are strongly arched and dipped into abdominal segment IX far anteriad of transverse sterno-styligeral impression (Figs 68–89, 111–112, 114–115, 117, 145).

Classification. The taxon Euthraulus/g1 is divided into plesiomorphon Euthraulus/g2 and holophyletic taxa Monophyllus/g(1) and Dilatognathus/g(1).

1.1.1.1.2.1. Plesiomorphon **Euthraulus/g2** Figs 68–116

Systematic position: Choroterpes/fg1—Choroterpes/fg2—Euthraulus/g1—pm.Euthraulus/g2.
Hierarchical name: Euthraulus/g2 (sine *Monophyllus*, *Dilatognathus*).
Possible rank-based names:
— genus *Euthraulus*;
— subgenus *Euthraulus*.

Character of unclear phylogenetic status.
(1) Tergalii II–VII are bilamellate (unlike *Monophyllus*); at each lamella all three apical processes [see Choroterpes/fg2 (2)] are subequal, long and slender (unlike *Dilatognathus*) (Figs 77–82, 99–105).

Discussion. The name *Thraululus* Ulmer, 1939 is regarded to be a junior synonym of *Euthraulus* [Gillies, 1957]. However, larva of the type species of *Thraululus* (*marginatus* Ulmer, 1913 [*Thraulus*]) is unknown, so this species cannot be identified as belonging to *Euthraulus* for certain.

Distribution and species composition. Distributed in Old World (Ethiopian, Oriental and Palaearctic Regions). The following described species belong here for certain: In West Palaearctic: *assimilis* Gaino et Sowa, 1985 [*Choroterpes* (*Euthraulus*)] (Greece); *balcanicus* Ikonomov, 1961 [*Euthraulus*] (Macedonia); *ortali* Sartori, 1992 [*Choroterpes* (*Euthraulus*)] (Israel); *caucasicus* **sp.n.** [*Choroterpes* (*Euthraulus*)] (Russian Caucasus); *sumbarensis* Kluge, 1984 [*Choroterpes* (*Euthraulus*)] (Turkmenistan); *arabica* Sartori et Gillies, 1990 [*Choroterpes* (*Euthraulus*)] (Saudi Arabia); *lindrothi* Peters, 1980 [*Choroterpes*] (= *mauritanicus* Soldán et Thomas, 1983 [*Choroterpes* (*Euthraulus*)]) (northern Africa). In East Palaearctic: *quadricus* Ali, 1967 [*Choroterpes*] (Pakistan); *altioculus* Kluge, 1984 [*Choroterpes* (*Euthraulus*)] (East Siberia and Far East); *anhuensis* Wu et You, 1992 [*Choroterpes*] (China). In Oriental Region: *alagarensis* Dinakaran et al., 2009 [*Choroterpes*] (India); *signata* Hagen, 1858 [*Cloe*] (Sri Lanka); *nanjingensis* You et al., 1979 [*Choroterpes* (*Euthraulus*)] (China); *taiwanensis* Kang et Yang, 1994 [*Choroterpes*] (Taiwan); *trifurcatus* Ueno, 1928 [*Choroterpes*] (Taiwan); *vittata* Nguyen et Bae, 2003 [*Choroterpes*] (Vietnam). In Ethiopian Region: *bugandensis* Kimmins, 1956 [*Euthraulus*]; *elegans* Barnard, 1932 [*Euthraulus*]; *starmuehlneri* Peters, 1980 [*Choroterpes* (*Euthraulus*)]; *usambarae* Gillies, 1957 [*Euthraulus*]. Species examined are reviewed below.

1.1.1.1.2.1-1. Euthraulus/g2 ***altioculus*** [***Choroterpes***] Figs 68, 70–73

Original binomen: *Choroterpes* (*Euthraulus*) *altioculus* Kluge, 1984.
Possible binomina:
— *Choroterpes* (*Euthraulus*) *altioculus*;
— *Euthraulus altioculus*.
REFERENCES: Kluge, 1984: male imago and larva.
MATERIAL. Holotype and paratypes [Kluge, 1984]: Primorskiy Kray, natural reserve "Kedrovaya Pad'", river Barabashevka (= Mongugay), 24.VI–10.VII.1980, coll. N. Kluge: 1 L-S-I♂ (holotype), 10 larvae; ibid., river Narva (= Sidime), 14–26.VII.1981, coll. N. Kluge: 1 L-S-I♂, 1 L-S-I♀, 8 larvae; natural reserve Lazovskiy, river Kievka, 16–20.VIII.1981, coll. N. Kluge: 3 larvae; river Ussuri near Novo-Chuguevka, 25.VIII.1980, coll. No. Kluge: 1 L-S-I♀.

Bauernfeind [1998] erroneously reported that holotype is "männchen Imago", while actually it represents larval, subimaginal and imaginal stages of the male specimen.

OTHER MATERIAL: RUSSIAN FEDERATION: Tomsk Province, river Mrassu near Tomsk, 16.VIII.1940, coll. V. Kruglova: 3 young larvae. Altai, Teletskoe Lake, 25.VI.1951, Yu. Zasypkina: 1 I(m). Kemerovo Province (Kuzbass): river Kaitan above village Sarbain, 29.VII.1949, coll. B. Rohdendorf: 1 young larva; Kuzdeevskiy Region, river Kaltranchik near village Sarbala, 12.VIII.1949 and VII.1950, coll. B. Rohdendorf: 5 larvae. Buryatia: river Vitim near Baisa, 24–27.VI.1969, coll. V. Zherikhin and E. Shitnikova: 3 I(m), 1 S(f); river Vitim near Ust'-Dzinta, 25.VII.1964: 1 larva; Rohoshino: 8 imagoes. Chita Province: river ingoda near Chita, 26.VI.1981, coll. N. Sinitshenkova: 1 larva; river Shilka near Sretensk, 29.VI.1948: 1 larva. Yakutia, summer house Bedzhiches, 1.VIII.1925, coll. L. Bianki: 1 I(m). KAZAKHSTAN: East Kazakhstan, river Ulban near Ust'-Kamenogorsk, 13–16.VI.1965, coll. I. Sukacheva: 25 larvae; river Ulda, 16.VI.1965, coll. I. Sukacheva: 3 larvae. JAPAN: pref. Hiroshima: Higashi-Hiroshima, river Kurose, 18.VI.2000, coll. I. Tatarenko: 2 larvae; Hiroshima-City, Uokiri, Asakita-ku, river Yoshiyama, 20.VII.2000, coll. I. Tatarenko: 2 larvae; river Tojo in Tojo, 20.IX.2000, coll. I. Tatarenko: 7 larvae; river Shiniogawa, 31.VIII.1917, coll. Roshkovskiy: 1 larva.

Larva. As described by Kluge [1984].

Subimago. Cuticular coloration: Cuticle of thorax at most light with brown sclerites; mesonotum at most brown;

most part of medioscutum and submedioscutum brown, posterior scutal protuberance brown except median part (as in Fig. 92). Cuticle of legs light brownish. Wings light brownish. Cuticle of abdomen light; cuticle of gonostyli brown.

Hypodermal coloration: Abdomen with brown maculation as in imago.

Texture: On each leg 1st tarsomere (shortened and fused with tibia) covered by microtrichiae of the same shape as microtrichiae on tibia; 2nd–5th tarsomeres covered by pointed microlepides.

Imago, male. As described by Kluge [1984]. Figure of genitals [Kluge, 1984: Fig. 8) is not accurate; correct one is given here (Fig. 68). Each penial projection [see Choroterpes/fg2 (3)] very long, sclerotized, pointed and armed by two narrow longitudinal flanges — median and dorsal ones; colorless spines small, located on edges of these flanges.

Egg. Chorion bears papillae and ridges going from one papilla to another [see Choroterpes/fg2 (1)] (Figs 70–73).

DIMENSION. Fore wing length 7–8 mm.

DISTRIBUTION. East Siberia, Russian Far East, Mongolia, Korea, Japan.

1.1.1.1.2.1-2. Euthraulus/g2 ***sumbarensis*** [***Choroterpes***] Figs 69, 74–75

Original binomen: *Choroterpes* (*Euthraulus*) *sumbarensis* Kluge, 1984.

Possible binomina:

— *Choroterpes* (*Euthraulus*) *sumbarensis*;

— *Euthraulus sumbarensis*.

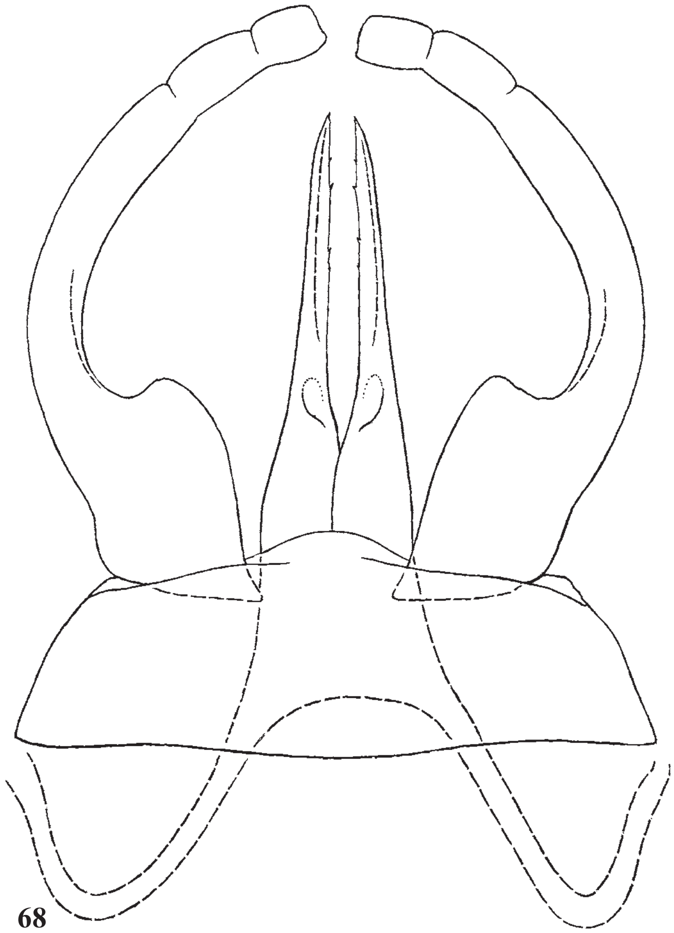
REFERENCES: Kluge, 1984: male imago and larva.

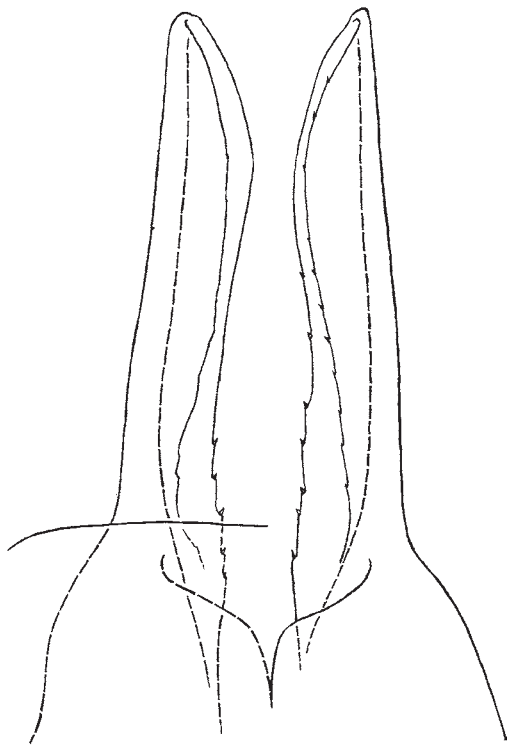
MATERIAL. Holotype and paratypes [Kluge, 1984]: Turkmenistan, river Sumbar near Karakala, 23–30.VI.1981, coll. N. Kluge: 1 L-S-I♀, 2 L-S♂, 8 larvae; river Ay-Dere near Ay-Dere, 1–5.VII.1981, coll. N. Kluge: 2 L-S-I♀, 28 larvae; river Sumbar near Ay-Dere, 5–10.VII.1981, coll. N. Kluge: 10 L-S-I♂ (among them holotype), 1 L-S-I♀, 2 L-S♂, 1 L-S♀, 12 larvae.

Bauernfeind [1998] erroneously reported that holotype is "männchen Imago", while actually it represents larval, subimaginal and imaginal stages of the male specimen.

Larva. As described by Kluge [1984].

Subimago. Cuticular coloration: Cuticle of thorax at most light; mesonotum at most light brownish, only sutures (anteronotal transverse impression, anterolateral scutal costa, antelateroparapsidal and lateroparapsidal sutures) darker


68


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Figs 68–69. *Choroterpes* spp.: 68 — *Ch.* (*Euthraulus*) *altioculus* (holotype), genitals of male imago (ventral view); 69 — *Ch.* (*E.*) *sumbarensis* (holotype), penis of male imago (ventral view; in the left — gonopore hidden by styliger, in the right — shown without styliger).

Рис. 68–69. *Choroterpes* spp.: 68 — *Choroterpes* (*Euthraulus*) *altioculus* (голотип), гениталии самца имаго (вентрально); 69 — *Ch.* (*E.*) *sumbarensis* (голотип), пенис самца имаго (вентрально; слева — гонопор скрыт стилигером, справа — показан без стилигера).

brown. Cuticle of legs light. Wings light brownish. Cuticle of abdomen colorless, cuticle of gonostyli light brownish.

Hypodermal coloration: Abdomen with brown maculation as in imago.

Texture: On each leg all tarsomeres covered by microtrichiae of the same shape as microtrichiae on tibia.

Imago, male. As described by Kluge [1984]. Each penis has proximal part so short, that at rest gonopores are hidden under styliger; apical projection [see Choroterpes/fg2 (3)] is unusually long, sclerotized and armed by two wide longitudinal flanges — median and medio-dorsal ones, each widened at its distal part; colorless spines small, locate on edges of these flanges (Fig. 69).

Egg. Chorion bears papillae and ridges going from one papilla to another [see Choroterpes/fg2 (1)] (Figs 74–75).

DIMENSION. Fore wing length 5–6 mm.

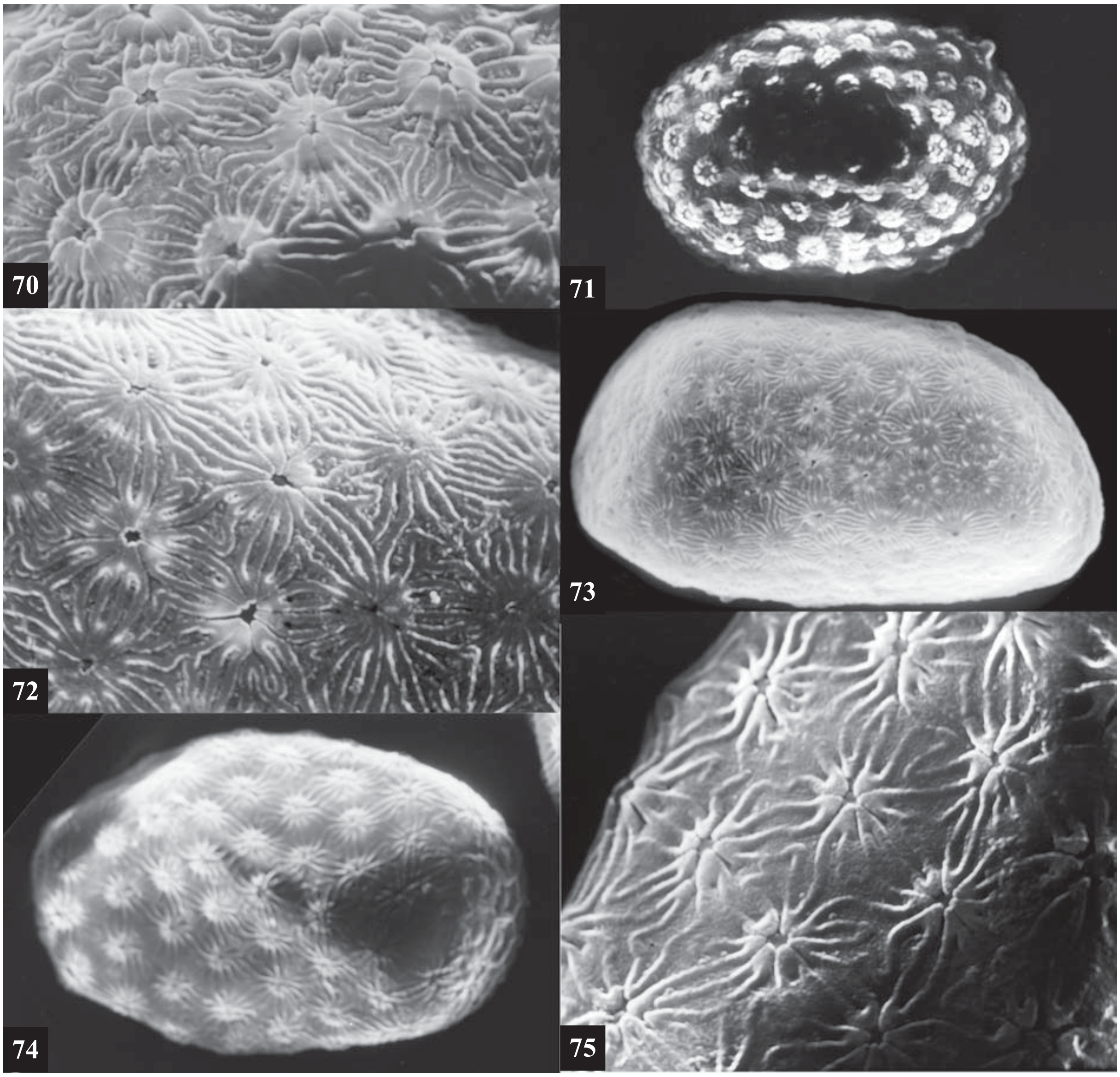
DISTRIBUTION. Kopetdag mountains in Turkmenistan.

1.1.1.1.2.1-3. Euthraulus/g2 *caucasicus* sp.n. [*Choroterpes*] Figs 76–97

Original binomen: *Choroterpes* (*Euthraulus*) *caucasicus* **sp.n.**
Possible binomina:
— *Choroterpes* (*Euthraulus*) *caucasicus*;
— *Euthraulus caucasicus*.

MATERIAL. Holotype: L-S-I♂ {specimen [A](21)88}: RUSSIA, Krasnodar Territory (= Krasnodarskiy Kray), river Psekups near railway station Chinary, 4.VI.1988, coll. N. Kluge. Paratypes: the same locality, 3–6.VI.1988, coll. N. Kluge: 5 L-S-I♂, 6 L-S-I♀, 1 L-S♀, 22 larvae; river Psekups railway station Goryaciy Kluch, 26–28.VIII.1985, coll. N. Kluge: 12 L-S-I♂, 11 L-S-I♀, 7 L-S♂, 6 L-S♀, 17 larvae; river Psekups railway station Fanagoriyskaya, 25–27.VIII.1991, coll. N. Kluge: 1 L-S-I♀, 8 larvae.

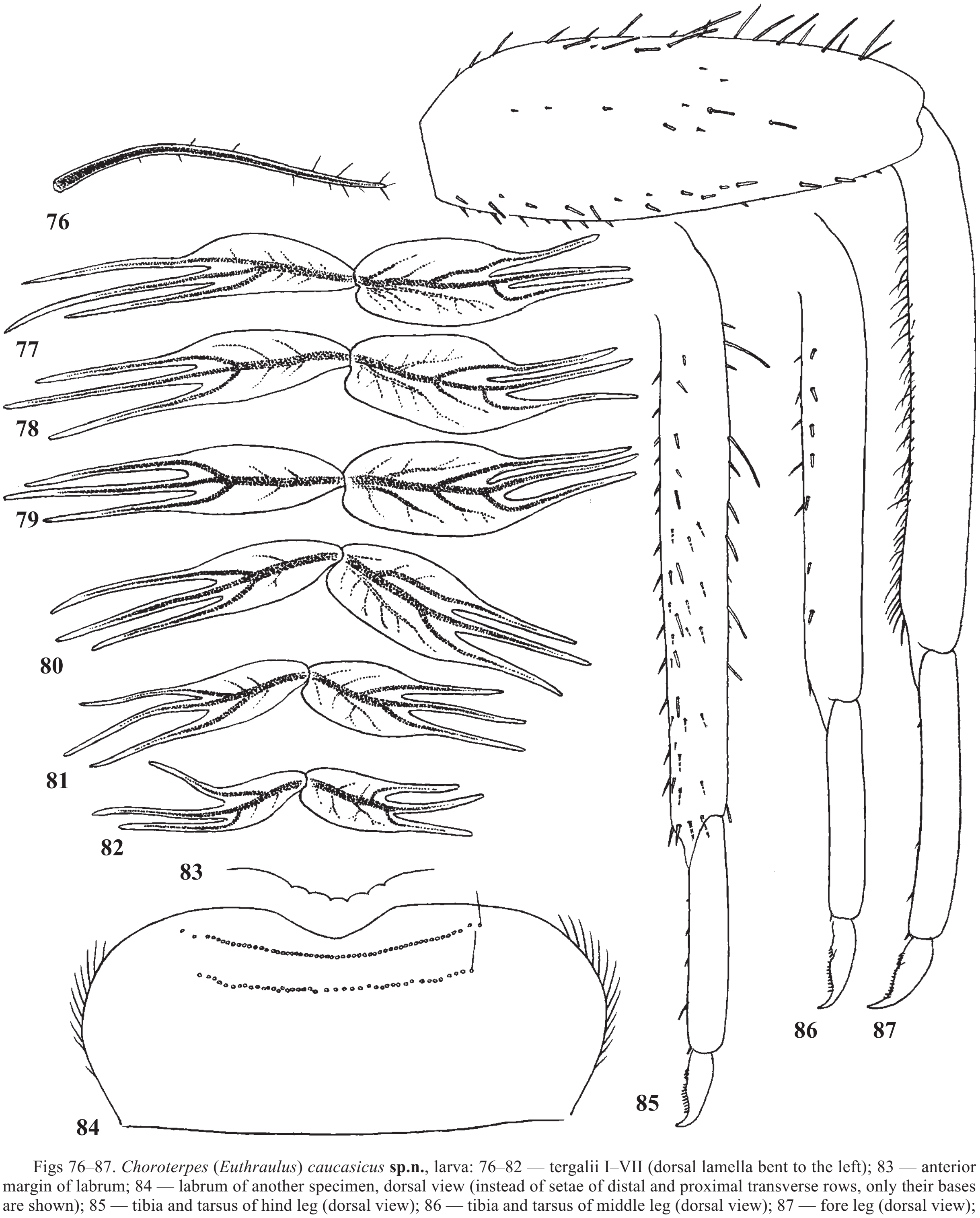
Larva. Cuticular coloration: Cuticle of head, pronotum and mesonotum light brownish, with diffusive markings; cuticle of legs and abdomen nearly colorless.



Figs 70–75. Euthraulus/g2, eggs: 70–73 — *Choroterpes* (*Euthraulus*) *altioculus*; 74–75 — *Ch.* (*E.*) *sumbarensis*.
Рис. 70–75. Euthraulus/g2, яйца: 70–73 — *Choroterpes* (*Euthraulus*) *altioculus*; 74–75 — *Ch.* (*E.*) *sumbarensis*.

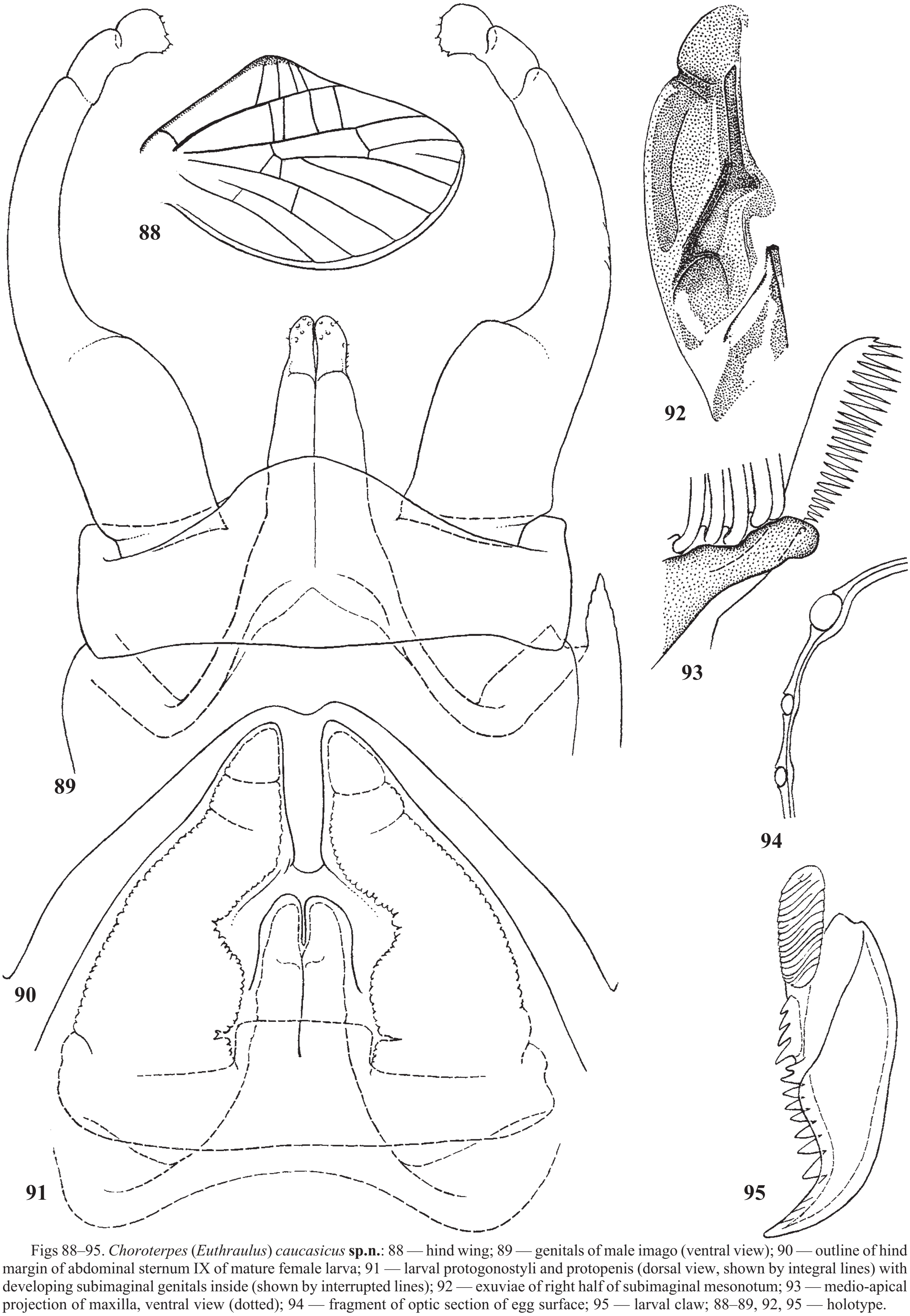
Hypodermal coloration: Abdominal terga with brown maculation as in imago.

Shape and setation: Labrum has median emargination moderate, with blunt denticles vestigial (Fig. 83) or absent (Fig. 84); distal transverse setal row regular; proximal transverse setal row regular, as wide as distal. Mandibles with outer margin moderately convex (similar to Fig. 44). Medio-apical projection of maxilla moderately expressed

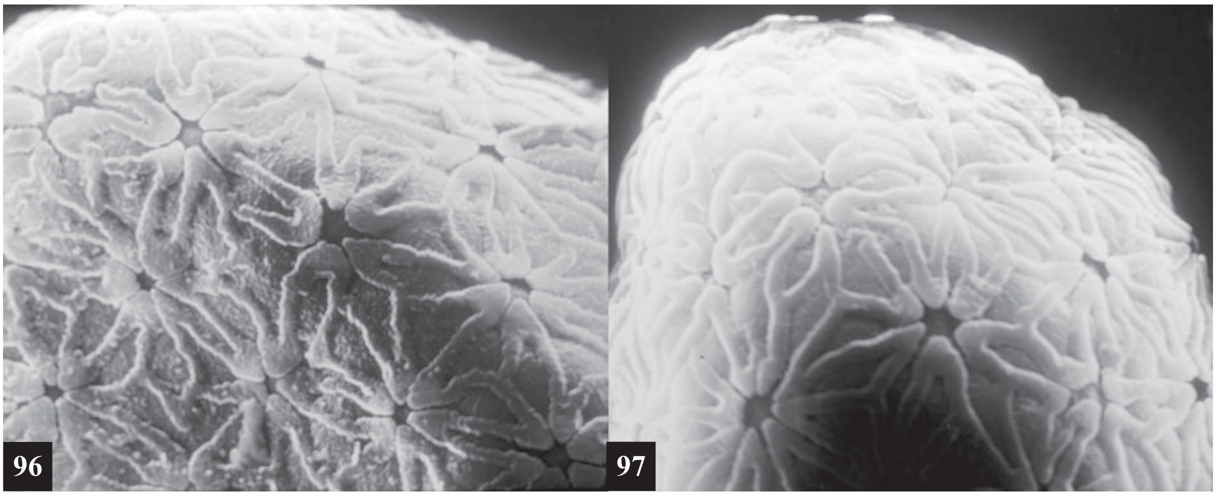


Figs 76–87. *Choroterpes* (*Euthraulus*) *caucasicus* **sp.n.**, larva: 76–82 — tergalii I–VII (dorsal lamella bent to the left); 83 — anterior margin of labrum; 84 — labrum of another specimen, dorsal view (instead of setae of distal and proximal transverse rows, only their bases are shown); 85 — tibia and tarsus of hind leg (dorsal view); 86 — tibia and tarsus of middle leg (dorsal view); 87 — fore leg (dorsal view); 76–82, 84–87 — holotype.

Рис. 76–87. *Choroterpes* (*Euthraulus*) *caucasicus* **sp.n.**, личинка: 76–82 — I–VII тергалии (дорсальный листок отогнут влево); 83 — передний край верхней губы; 84 — верхняя губа другого экземпляра, дорсально (вместо щетинок дистального и проксимального поперечных рядов показаны только их основания); 85 — голень и лапка задней ноги (дорсально); 86 — голень и лапка средней ноги (дорсально); 87 — передняя нога (дорсально); 76–82, 84–87 — голотип.



Figs 88–95. *Choroterpes* (*Euthraulus*) *caucasicus* **sp.n.**: 88 — hind wing; 89 — genitals of male imago (ventral view); 90 — outline of hind margin of abdominal sternum IX of mature female larva; 91 — larval protogonostyli and protopenis (dorsal view, shown by integral lines) with developing subimaginal genitals inside (shown by interrupted lines); 92 — exuviae of right half of subimaginal mesonotum; 93 — medio-apical projection of maxilla, ventral view (dotted); 94 — fragment of optic section of egg surface; 95 — larval claw; 88–89, 92, 95 — holotype.



Figs 96–97. *Choroterpes* (*Euthraulus*) *caucasicus* **sp.n.**, eggs.
Рис. 96–97. *Choroterpes* (*Euthraulus*) *caucasicus* **sp.n.**, яйца.

(Fig. 93). Femur of fore leg widest proximally (Fig. 87), femora of middle and hind legs widest at middle (similar to Fig. 27). Femora with irregularly situated stout blunt setae of various length. Pectinate setae on ventral side of hind femur pointed and curved, form a single irregular row parallel to inner margin of femur. Stout setae on inner side of fore tibia situated densely and irregularly, bipectinate (pointed, with two rows of stout pointed processes by sides). Inner side of middle and hind tibia with a sparse row of stout setae; outer side of hind tibia with stout setae of variable length, as on outer side of femur. Outer sides of all tibiae with irregularly situated thin hairs, whose length exceed tibia width (not shown in Figs 85–87). Abdomen without stout setae. Posterolateral spines expressed on abdominal segment VII–IX. Hind margins of abdominal terga with pointed denticles, whose size increases from tergum I to tergum X; sterna without denticles. Tergalii II–VII [see *Euthraulus* (1)] have all three processes of both lamellae well developed; anal-proximal projection of ventral lamella poorly expressed (Figs 77–82). Protogonostyli of male larva narrowly separated; protopenes convergent, completely hidden under sternum XI (Fig. 91). Female larva has hind margin of abdominal sternum IX slightly incised (Fig. 90).

Subimago. CUTICULAR COLORATION: Cuticle of thorax at most light with brown sclerites; mesonotum at most brown: most part of medioscutum brown, most part of submedioscutum somewhat lighter brown, posterior scutal protuberance brown except median part (Fig. 92). Cuticle of legs light brownish. Wings light brownish. Cuticle of abdomen colorless, cuticle of gonostyli brown.

HYPODERMAL COLORATION: Abdomen with brown maculation as in imago.

TEXTURE: On fore leg 1st tarsomere (shortened and fused with tibia) covered by microtrichiae of the same shape as microtrichiae on tibia; 2nd–5th tarsomeres covered by pointed microlepides. On middle and hind legs 1st–4th tarsomeres covered by microtrichiae of the same shape as microtrichiae on tibia; 5th tarsomere covered by pointed microlepides.

Imago, male. Head brown; dorsal eyes not elevated [as in Kluge, 1984: Fig.22], brownish-orange. Thorax brown with ocher. On fore wing basal sclerites brownish, veins light, membrane colorless; pterostigma whitish, with simple oblique crossveins. Hind wing with costal projection blunt (Fig. 88). Legs light brownish; on each leg cuticle of extreme femur base and knee area (apex of femur and base of tibia) colored by darker brown. Each abdominal tergum with a pair of large diffusive dark brown hypodermal maculae, which occupy its most part except for ocher stripe bordering anterior margin, ocher stripe bordering posterior margin, ocher medial longitudinal stripe and ocher areas laterad of tracheal trunks. Sterna I–VIII uniformly ocher, last abdominal ganglion tinged with dark brown. Abdominal sternum IX with styliger has middle part ocher, periphery areas (anterior, posterior and lateral) brown. Gonostyli light, ocher. 1st+2nd segments of gonostylus with inner margin convex. Penes brown; each penis has apical projection [see Choroterpes/fg2 (3)] not long, with apex roundish; its denticles are very small (Fig. 89). Caudalii light.

Imago, female. Coloration as in male. Posterior plate of abdominal sternum IX apically slightly incised, as in larva (as in Fig. 90).

Egg. Yellow, oval. Chorion bears evenly dispersed papillae and ridges going from one papilla to another [see Choroterpes/fg2 (1)]; papillae small (Figs 96–97), one pole bears larger papillae (Fig. 94).

DIMENSION. Fore wing length 5–6 mm.

DISTRIBUTION. Western Caucasus.

COMPARISON. In larval and adult structure *Ch.* (*E.*) *caucasicus* **sp.n.** is similar to *Ch.* (*E.*) *assimilis* Gaino et Sowa, 1985 (whose male imago is unknown). Unlike *Ch.* (*E.*) *caucasicus* **sp.n.** and most other species of *Choroterpes*, *Ch.* (*E.*) *assimilis* has no characteristic relief on egg surface [see Choroterpes/fg2 (1)].

←

Рис. 88–95. *Choroterpes* (*Euthraulus*) *caucasicus* **sp.n.**: 88 — заднее крыло; 89 — гениталии самца имаго (вентрально); 90 — очертание заднего края IX стернита брюшка зрелой личинки самки; 91 — протогоностили и протопенис личинки (дорсально, показаны сплошными линиями) с развивающимися субимагинальными гениталиями внутри (показаны прерывистыми линиями); 92 — экзувий правой половины субимагинального мезонотума; 93 — медио-апикальный выступ максиллы, вентрально (пунктирован); 94 — участок оптического среза поверхности яйца; 95 — коготок личинки; 88–89, 92, 95 — голотип.

1.1.1.1.2.1-4. Euthraulus/g2 ***signata*** [***Cloe***]
Figs 98–116

Original binomen: *Cloe signata* Hagen, 1858.
Possible binomina:
— *Choroterpes* (*Euthraulus*) *signatus*;
— *Euthraulus signatus*.

REFERENCES: Eaton, 1883–1888: imago and subimago (*Thraulus signatus*).

MATERIAL. Sri Lanka, coll. N. Kluge & L. Sheyko: boundar- between Uva province and Central province, tributary of river Uma near Randenigala dam, 13–14.I.2011: 1 L-S-I♂, 1 L-S-I♀, 16 larvae. Uva province, Badulla district, Haputale Forest and river Lemastota Oya, 15–23.I.2011: 5 L-S-I♂, 3 L-S-I♀, 2 L-S♀, 20 larvae. Sabaragamuwa province, river Seetha Sangula, Dalhausie near Sri Pada (Adam's Peak), 24–26.I.2011: 14 larvae. Central province, river Mahaveli Ganga in Ginigathhena (17 km N Hatton), 31.I–3.II.2011: 1 L-S-I♂.

Larva. Cuticular coloration: Cuticle of head, thoracic terga and pleura brown with contrasting ocher blanks; cuticle of thoracic sterna light. Cuticle of legs variable, either uniformly light, or with dark maculae: femur can have large macula in middle and large macula near apex; hind femur can have longitudinal macula stretching from femur base to the middle macula; tibia can be darkened near base; tarsus can be dark except extreme base and distal part. Cuticle of abdominal terga variable, either uniformly light, or with contrasting dark ornament adjacent to fore, hind and/or lateral margins of each or some terga. Cuticle of abdominal sterna either uniformly light or with dark maculae adjacent to fore margins of some sterna.

Hypodermal coloration: Head, thorax and abdomen with brown maculation. Each femur pale, with dark brow maculae in middle and near apex, as in imago. Color of tergalii variable: either nearly colorless, or dark gray, with dorsal lamella nearly black.

Shape and setation: Labrum not wide, its median emargination rather deep, with blunt denticles; distal transverse setal row regular; proximal transverse setal row regular, narrower than distal (Fig. 107). Mandibles with outer margin moderately convex (Fig. 110). Medio-apical projection of maxilla moderately expressed (similar to Fig. 93). Femur of fore leg widest proximally, femora of middle and hind legs widest at middle (similar to Figs 24, 27). Pectinate setae on ventral side of hind femur pointed and curved, form a stripe parallel to inner margin of femur (similar to Figs 150–151). Stout setae on inner side of fore tibia dense and arranged in 3 nearly regular rows (as in Fig. 25), pointed and bipectinate (with two rows of stout pointed processes by sides). Inner side of middle and hind tibia with a sparse row of stout setae; outer side of hind tibia with stout setae of variable length, as on outer side of femur. Outer sides of all tibiae with irregularly situated thin hairs, whose length exceed tibia width. Abdomen without stout setae. Posterolateral spines well expressed on abdominal segments beginning from IV–VI to IX. Posterolateral spines on terga VIII and IX have inner convexities very prominent, often projected caudally (Figs 108, 109). Hind margins of abdominal terga with pointed denticles, whose size increases from tergum I to tergum X; sterna without denticles. Tergalii II–VI [see *Euthraulus* (1)] have all three processes of both lamellae well developed; tergalius VII variable: dorsal lamella has costal process either vestigial (Fig. 104) or well-developed (Fig. 105); ventral lamella has all three processes well developed. Costal and ventral processes of ventral lamella widened proximally. Anal-proximal projection of ventral lamella poorly expressed on tergalius II, very prominent on tergalii III–VII (Figs 99–104). Protogonostyli of male larva narrowly separated; protopenes convergent, completely hidden under sternum XI (similar to Fig. 91). Female larva has hind margin of abdominal sternum IX slightly incised (similar to Fig. 90).

Subimago. Cuticular coloration: Cuticle of thorax at most light with brown sclerites; mesonotum at most brown; most part of medioscutum and submedioscutum brown, posterior scutal protuberance brown except median part (as in Fig. 92). Cuticle of legs light brownish. Wings light brownish. Cuticle of abdominal terga light brownish; abdominal sterna I–VIII colorless; sternum IX brown anteriorly and laterally, with colorless semicircular area medially-posteriorly; cuticle of gonostyli brown.

Hypodermal coloration: Abdomen and femora with brown maculation as in imago.

Texture: On each leg 1st tarsomere (shortened and fused with tibia) covered by microtrichiae of the same shape as microtrichiae on tibia; 2nd–5th tarsomeres covered by pointed microlepides.

Imago, male. Head brown; dorsal eyes not elevated [as in Kluge, 1984: Fig.22], brownish-orange. Thorax brown with ocher. On fore wing basal part, including costal brace, brown, other membrane colorless; veins light; pterostigma whitish, with 4–7 simple crossveins. Hind wing with costal projection blunt (Fig. 106). Each leg has cuticle colorless, with knee area (apex of femur and base of tibia) light brown; hypodermal pigmentation forms wide black band at middle of femur, wide black band at apex of femur, sometimes black spot in proximal half of femur, sometimes small band near apex of tibia; sometimes tibia and tarsus brown. Abdominal terga at most dark brown, with darker and lighter areas repeated on terga I–IX. Sterna I–VIII lighter, last abdominal ganglion tinged with dark brown. Abdominal sternum IX brown anteriorly and laterally, with colorless semicircular area medially-posteriorly; styliger and gonostyli brown. Styliger strongly narrows from base toward apex; 1st+2nd segments of gonostylus with inner margin convex. Penes brown; each penis has apical projection [see Choroterpes/fg2 (3)] moderately long, conic, slightly bent medially-dorsally; its denticles are very small. In other respects genitals are quite variable: posterior margin of styliger varies from slightly concave (Fig. 115) to strongly convex (Fig. 111); thick proximal part of gonostylus varies from long and smoothly projected (Figs 114–115) to short and sharply projected (Figs 111–112); shape of penis is rather variable. Caudalii light, with dark brown ring at each joining.

Imago, female. Coloration as in male. Posterior plate of abdominal sternum IX with small apical incision.

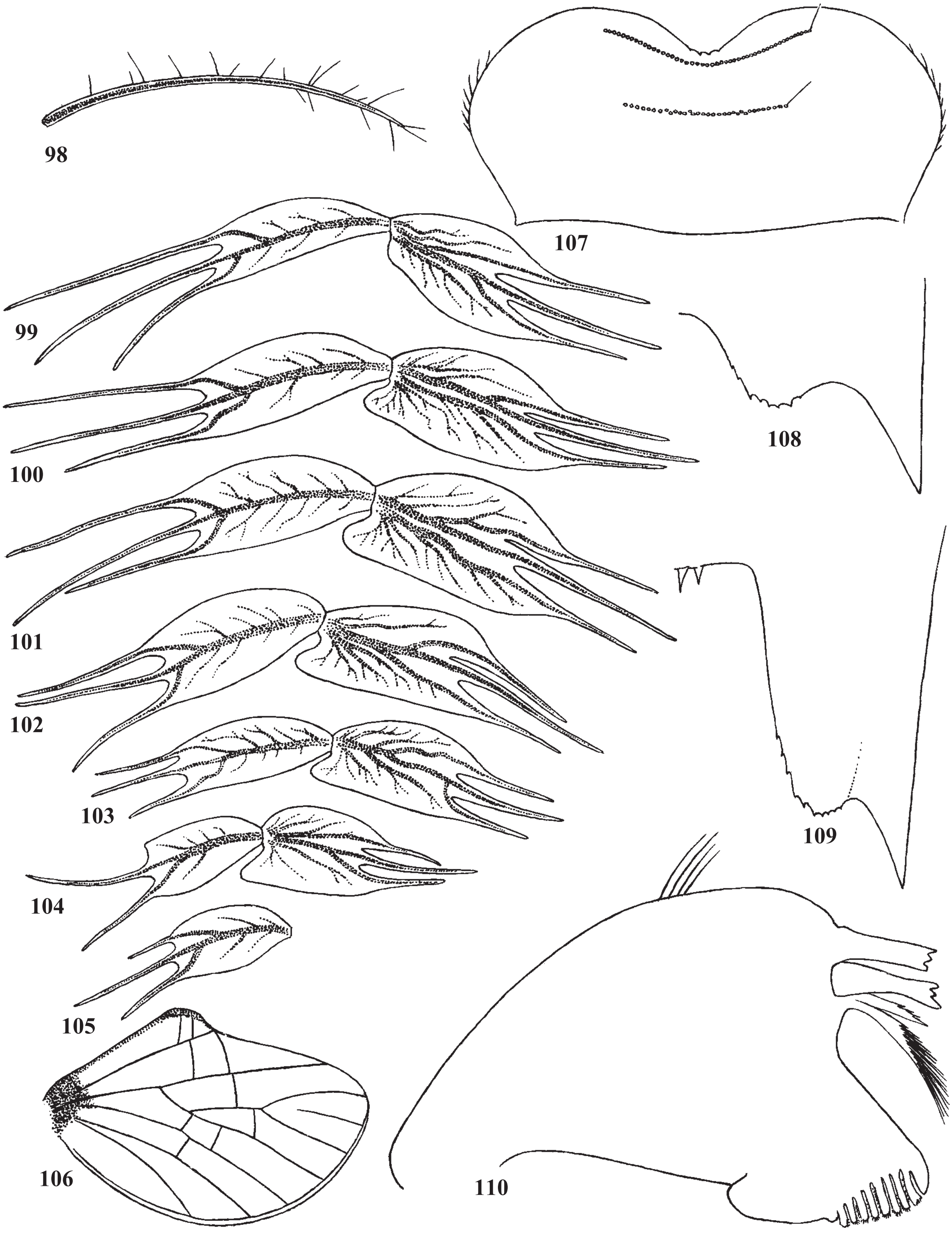
Egg. Yellow, oval. Chorion bears evenly dispersed papillae and ridges going from one papilla to another [see Choroterpes/fg2 (1)]; papillae small, one pole bears larger papillae.

DIMENSION. Variable, fore wing length 4–7 mm.

DISTRIBUTION. Sri Lanka.

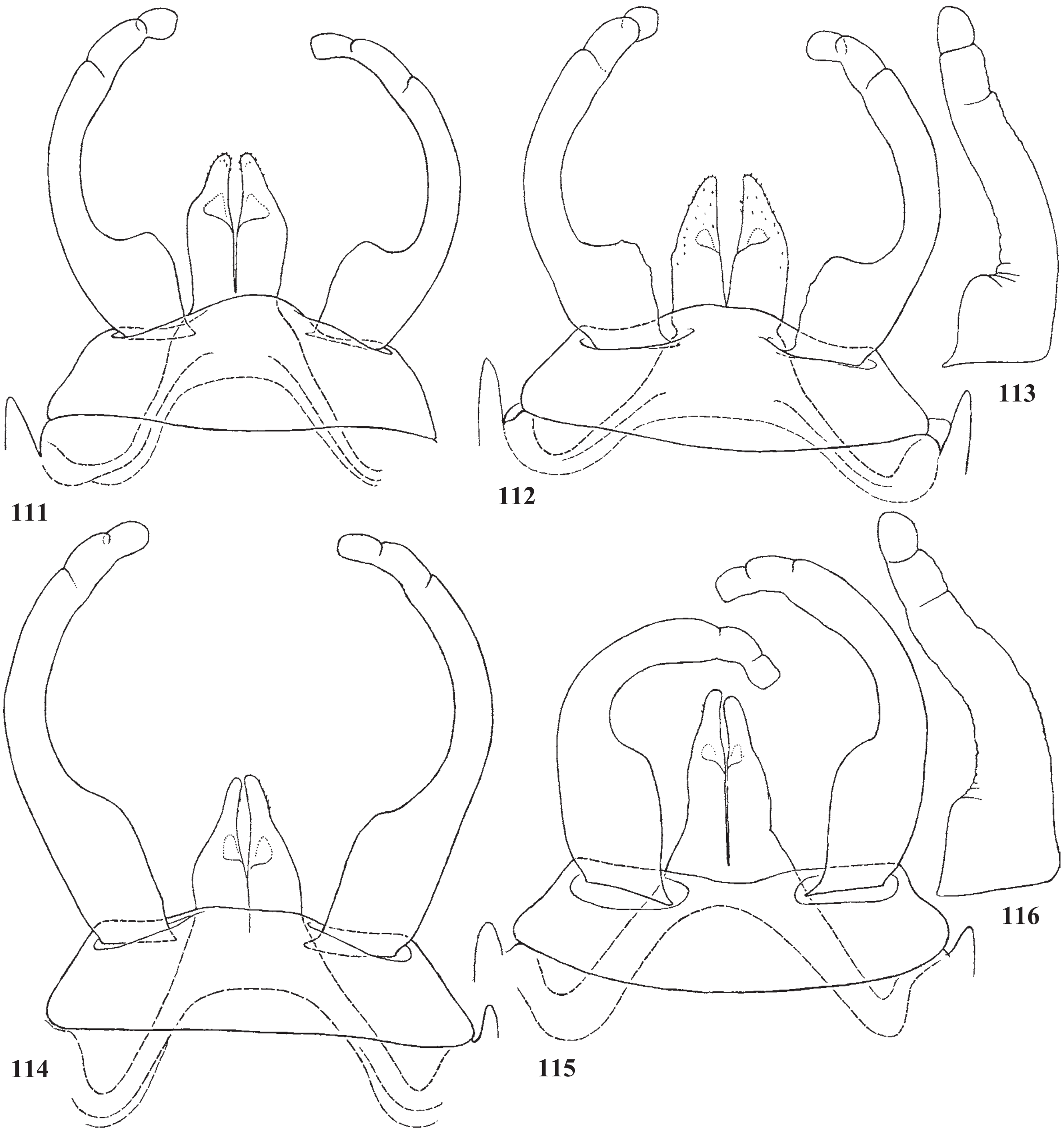
COMMENTS. *Ch.* (*E.*) *signatus* has great individual variability in size, cuticular coloration of larval abdomen and legs, hypodermal coloration of tergalii, shape of male imaginal styliger, gonostyli and penis. Comparison of 7 male imagoes reared from larvae allows to conclude that they belong to a single species. In subimaginal stage individual variability of gonostyli shape is less than in imaginal stage (compare Figs 112 and 113; 115 and 116).

Eaton [1883–1888] reported that with the type specimens of *Cloe signatus* stood two specimens of two other species, numbered 32 and 37. Judging by his descriptions, the specimen No.32 can belong to *Megaglena brincki* Peters et Edmunds, 1970. Systematic position of the specimen 37, whose femora are colorless, is unclear.



Figs 98–110. *Choroterpes* (*Euthraulus*) *signatus*: 98–104 — tergalii I–VII (dorsal lamella bent to the left); 105 — dorsal lamella of tergalius VII, another specimen; 106 — hind wing; 107 — labrum, dorsal view (instead of setae of distal and proximal transverse rows, only their bases are shown); 108–109 — posterolateral spines of larval abdominal terga VIII and IX; 110 — left mandible.

Рис. 98–110. *Choroterpes* (*Euthraulus*) *signatus*: 98–104 — I–VII тергалии (дорсальный листок отогнут влево); 105 — дорсальный листок VII тергалии, другой экземпляр; 106 — заднее крыло; 107 — верхняя губа, дорсально (вместо щетинок дистального и проксимального поперечных рядов показаны только их основания); 108–109 — постеролатеральные шипы VIII и IX тергитов брюшка личинки; 110 — левая мандибула.



Figs 111–116. *Choroterpes* (*Euthraulus*) *signatus*, genitals of male imagoes reared from larvae: 111 — from River Uma; 112 — from Ginigathhena; 113 — subimaginal gonostylus of the same specimen; 114–115 — from Haputale; 116 — subimaginal gonostylus of the same specimen.

Рис. 111–116. *Choroterpes* (*Euthraulus*) *signatus*, гениталии самцов имаго, выведенных из личинок: 111 — из реки Ума; 112 — из Гинигатхены; 113 — субимагинальный гоностиль того же экземпляра; 114–115 — из Хапутале; 116 — субимагинальный гоностиль того же экземпляра.

1.1.1.1.2.1-5. Euthraulus/g2 ***bugandensis*** [***Euthraulus***]

Original binomen: *Euthraulus bugandensis* Kimmins 1956**.**

Possible binomina:

— *Choroterpes* (*Euthraulus*) *bugandensis*;

— *Euthraulus bugandensis*.

REFERENCES: Kimmins, 1956: imago; Sartori & Gillies, 1990: larva and egg.

MATERIAL. Uganda, Victoria Nile at Bujagali Falls, 6–7.VII.2007, coll. N. Kluge: 4 S-I♂, 1 S♂, 1 S-I♀, 1 I♀, 3 larvae. Lake Viktoria, Jinja, 6–10.VII.2007, coll. N. Kluge: 1 S-I♂, 2 I♂.

1.1.1.1.2.2. **Monophyllus/g(1)**, or ***Monophyllus***
Figs 117–128

Systematic position: Choroterpes/fg1—Choroterpes/fg2—Euthraulus/g1—*Monophyllus*.

Hierarchical typified name: Monophyllus/g(1) [g: *Monophyllus* Kluge, **subgen.n.**; type species: *Choroterpes* (*Monophyllus*) *monophyllus* Kluge, **sp.n.**].

Possible rank-based names:

— subgenus *Monophyllus* in genus *Choroterpes*;

— subgenus *Monophyllus* in genus *Euthraulus*;

— genus *Monophyllus*.

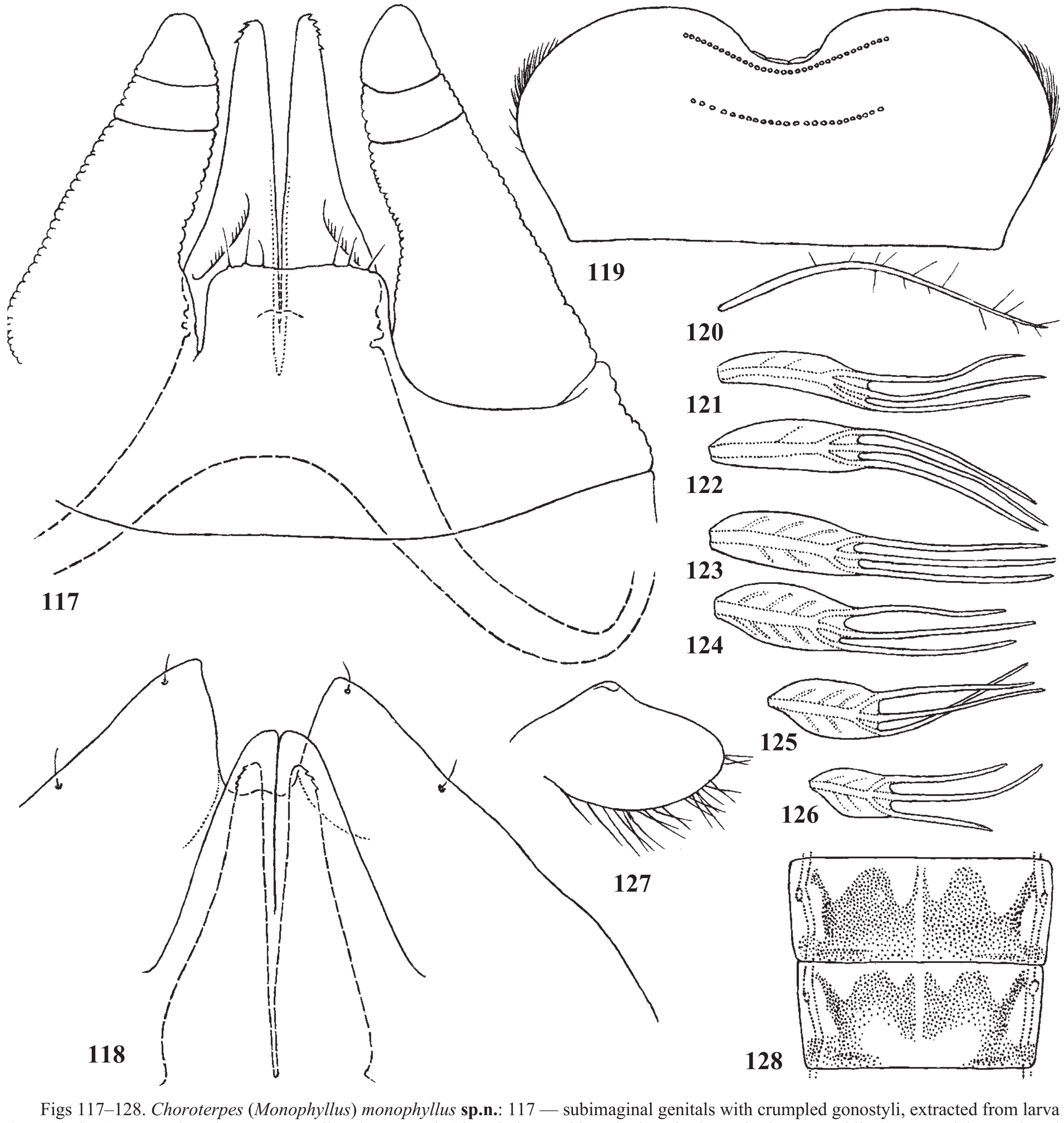
Autapomorphy.

(1) Tergalii II–VII [initially bilamellate — see Choroterpes/fg2 (2)] are unilamellate. Each lamella has all three apical processes subequal, long and slender (Figs 121–126) (as in *Euthraulus*).

Distribution and species composition. A single species is known from Hainan Island.

1.1.1.1.2.2-1. Monophyllus/g(1) ***monophyllus*** **sp.n.** [***Choroterpes***] Figs 117–128

Original binomen: *Choroterpes* (*Monophyllus*) *monophyllus* **sp.n.**
Possible binomina:
— *Choroterpes* (*Monophyllus*) *monophyllus*;
— *Choroterpes* (*Euthraulus*) *monophyllus*;
— *Euthraulus* (*Monophyllus*) *monophyllus*;
— *Monophyllus monophyllus*.



Figs 117–128. *Choroterpes* (*Monophyllus*) *monophyllus* **sp.n.**: 117 — subimaginal genitals with crumpled gonostyli, extracted from larva (ventral view); 118 — larval protogonostyli and protopenis (dorsal view; subimaginal penis shown by interrupted line); 119 — labrum, dorsal view (instead of setae of distal and proximal transverse rows, only their bases are shown); 120–126 — tergalii I–VII; 127 — outline of subimaginal hind wing, extracted from larva and spread; 128 — hypodermal coloration of abdominal terga VI and VII; 117, 119–128 — holotype.

Рис. 117–128. *Choroterpes* (*Monophyllus*) *monophyllus* **sp.n.**: 117 — субимагинальные гениталии со смятыми гоностилями, отпрепарированные из личинки (вентрально); 118 — личиночные протогоностили и протопенис (дорсально; субимагинальный пенис показан прерывистой линией); 119 — верхняя губа, дорсально (вместо щетинок дистального и проксимального поперечных рядов показаны только их основания); 120–126 — I–VII тергалии; 127 — очертание субимагинального заднего крыла, отпрепарированного из личинки и расправленного; 128 — гиподермальная окраска VI и VII тергитов брюшка; 117, 119–128 — голотип.

MATERIAL. Holotype: L/S♂, China, Hainan, Miao-Li, 19.XII.1957, coll. N. Andrianova. Paratypes: the same locality, 2 male larvae.

Larva. Cuticular coloration: Cuticle of head, pronotum and mesonotum brown, with diffusive markings; cuticle of legs and abdomen light brownish, nearly unicolorous, without contrasting markings.

Hypodermal coloration: Legs light; each femur with a dark brown spot at middle and a dark brown band near apex; fore femur also with a brown spot near base. Each abdominal tergum II–VI at most part brown with lighter blanks adjacent to anterior margin; each tergum VII–IX, besides anterior blanks, with a pair of large blanks adjacent to posterior margin (Fig. 128).

Shape and setation: Labrum not wide, its median emargination rather deep, with blunt denticles; both distal and proximal transverse setal rows regular (Fig. 119). Mandibles with outer margin moderately convex (similar to Fig. 110). Medio-apical projection of maxilla moderately expressed (similar to Fig. 93). Femur of fore leg widest proximally, femora of middle and hind legs widest at middle (similar to Figs 24, 27). Femora with irregularly situated stout setae of various length. Ventral side of hind femur with irregularly situated curved pectinate setae (similar to Figs 150–151). Stout setae on inner side of fore tibia dense and arranged in 3 nearly regular rows (as in Fig. 25), pointed and pectinate. Inner side of middle tibia with 2 or 1 stout setae. Inner side of hind tibia with a sparse row of stout setae; outer side of hind tibia with stout setae of variable length, as on outer side of femur (similar to Fig. 85). Outer sides of all tibiae with irregularly situated thin hairs, whose length exceed tibia width. Abdomen without stout setae. Posterolateral spines short and obtuse. Hind margins of abdominal terga with pointed denticles, whose size increases from tergum I to tergum X; sterna without denticles. Tergalii unilamellate (Figs 120–126). Protogonostyli of male larva narrowly separated; protopenes convergent, narrowed toward apex, long, projected between protogonostyli (Fig. 118).

Subimago (extracted from mature larva). Cuticular coloration: Cuticle of thorax at most light with brown sclerites; mesonotum at most brown; most part of medioscutum and submedioscutum brown, posterior scutal protuberance brown except median margin (as in Fig. 92). Fore and hind wings light, with dark brown spot near base, including costal brace.

Hypodermal coloration: Femora and abdomen with hypodermal coloration as in larva.

Texture: On each leg 1st tarsomere (shortened and fused with tibia) covered by microtrichiae of the same shape as microtrichiae on tibia; 2nd–5th tarsomeres covered by pointed microlepides.

Imago male. Unknown. Judging by subimaginal genitals, extracted from larva, each penis has apical projection [see Choroterpes/fg2 (3)] long, and conic; its denticles are relatively large, located on tip of penis and directed proximally (Fig. 117).

Female. Unknown.

Egg. Unknown.

DIMENSION. Fore wing length 4 mm.

DISTRIBUTION. Hainan Island.

1.1.1.1.2.3. **Dilatognathus/g(1)**, or ***Dilatognathus***
Figs 129–133

Systematic position: Choroterpes/fg1—Choroterpes/fg2—Euthraulus/g1—*Dilatognathus*.

Hierarchical typified name: Dilatognathus/g(1) [g: *Dilatognathus* Kluge, **subgen.n.**; type species: *Choroterpes* (*Dilatognathus*) *cataractae* Kluge, **sp.n.**].

Possible rank-based names:
— subgenus *Dilatognathus* in genus *Choroterpes*;
— subgenus *Dilatognathus* in genus *Euthraulus*;
— genus *Dilatognathus*.

Autapomorphies.

(1) Mouth apparatus has following modifications:

Labrum is widened, its median incision (characteristic for Atalophleboculata) is widened; proximal transverse row of setae (characteristic for Atalophlebopectinata) is shifted to proximal part of labrum and can be interrupted medially (Fig. 133).

Maxilla has inner-apical angle produced as tusk-like process; pectinate setae of ventro-apical row (characteristic for Leptophlebia/fg1) are vestigial and located on the tusk-like process (Fig. 131). In other respects maxilla differs in young larvae and in ultimolarva:

In young larva the single pectinate dentiseta [see Atalophlebomaxillata (2)] is straightened and parallel to the tusk-like process; the ventro-apical flange [see Atalophlebomaxillata (1)] is shortened (Fig. 132).

In ultimolarva (i.e., last-instar larva, or nymph) the tusk-like process is long, the dentiseta is lost and the ventro-apical flange is very low and poorly expressed (Fig. 129).

Maxillary palp is elongate and bears long filtering setae: 2nd segment in apical part of inner side has a few such setae forming a longitudinal row; 3rd (terminal) segment has a proximal semicircular transverse row of such setae on its inner side and fields of irregularly situated setae along its ventral and dorsal sides (Figs 130–131).

Labium has paraglossae widened, expanded laterally [Peters & Edmunds, 1970: Fig. 165]. Labial palp is elongate and bears long filtering setae which form regular longitudinal rows: 2nd segment has a double row on outer side and a row on dorsal side; 3rd segment has a row on outer side and a row on inner side; dorsal side of 3rd segment also bears smaller irregularly situated setae (Fig. 139).

(2) Tergalius I [initially different from others – see Choroterpes/fg1 (1)] is lost, thus only tergalii II–VII are present [see (3)].

(3) Tergalii have the same structure in all species (Figs 138, 140, 141). Each of two lamellae of tergalii II–VII is widened, its 3 apical processes [see Choroterpes/fg2 (2)] are brought together, side processes of ventral lamella are wide basally. Each tergalius II–VI normally has all 6 apical processes (only in individual cases some processes can be absent); tergalius VII has 5 apical processes only: its dorsal lamella has no costal process (Fig. 138). Tergalii II–V have equal size and shape, tergalius VI is smaller, tergalius VII (with 5 apical processes) is the smallest.

Discussion: status of the generic name *Choroterpides.* Larvae of the taxon described here as *Dilatognathus* **subgen.n.**, are known under the generic name *Choroterpides* Ulmer, 1939. Ulmer [1939] established this genus basing on imagoes and larvae, which he attributed to two species — *Choroterpides exigua* (Eaton, 1884) and *Choroterpides major* Ulmer, 1939. According to original designation [Ulmer, 1939: 495], the type species of *Choroterpides* is *Ch. exigua* (originally *Thraulus exiguus* Eaton, 1884, but not *Choroterpes exiguus* Eaton, 1892). Originally, *Thraulus exiguus* was described from "Lahat, Palembang" in southern Sumatra; its type specimen is lost [Ulmer, 1939; Kimmins, 1960]. Ulmer's description of "*Choroterpides exigua*" is based on specimens from Java (mainly from Buitenzorg, now Bogor) and southern Sumatra. His figures of male imaginal genitals [Ulmer, 1939: figures 40 and 41] are different from the original description: in the original description [Eaton, 1883–1888: Pl. 13, Fig. 20*2] styliger is strongly convex; last segment of gonostylus is very small (much narrower than previous seg-

ments); penis is very small (shorter than widened part of gonostylus) and strongly narrowed in the middle. There is no reason to regard the male imagoes describes by Eaton and Ulmer as belonging to the same species. Recently, most Indonesian species of mayflies remain to be undescribed, so the type of *Thraulus exiguus* can belong to a species which has not been rediscovered yet. Ulmer had no reared male imagoes, so his association of larvae and imagoes of two species is not grounded. The taxon *Choroterpides*, as described by Ulmer, is well characterized by larval structure (specialized mouth apparatus and characteristic structure of tergalii), but has no sufficient diagnosis for adults. So the original description of *Choroterpides* should be regarded as based on misidentified type species. According to the Article 70.3 of the International Code of Zoological Nomenclature, "If an author discovers that a type species was misidentified ... the author may select, and thereby fix as type species, the species that will, in his or her judgment, best serve stability and universality, either (70.3.1.) the nominal species previously cited as type species [Arts. 68, 69], or (70.3.2.) the taxonomic species actually involved in the misidentification". As no one species has been sufficiently described basing on reared material, I am fixing as the type species of *Choroterpides* the nominal species previously cited as type species — i.e., the species described by Eaton as *Thraulus exiguus*. According to this type fixation, the generic name *Choroterpides* belongs to a taxon of unclear systematic position. Judging by strongly convex styliger, it can belong to the plesiomorphon Euthraulus/g2; in this case *Choroterpides* Ulmer, 1939 is a junior synonym of *Euthraulus* Barnard, 1932.

Originally, the genus *Choroterpides* was characterized by imaginal and larval characters; its imago was opposed to *Choroterpes* as having narrower hind wings and 3-segmented gonostyli, while *Choroterpes* was regarded to have 4-segmented gonostyli [Ulmer, 1939]. Actually, number of gonostyli segments is the same (see Discussion on Choroterpes/fg2 above). Hind wing of *Choroterpes* s.str. have variable width and shape.

Peters and Edmunds [1970] suggested to separate imagoes of *Choroterpides* by a single character — presence of a distance between posterior margin of fore wing and a vein bordering this margin. Actually this distance is present in all Choroterpes/fg2 (Figs 40, 50, 88, 106, 136) [Kluge, 1984: Figs 6, 25].

Distribution and species composition. Oriental Region. *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.** from Lombok is described below. The species originally described from Java as *Choroterpides major* Ulmer, 1939, belongs to *Dilatognathus* — *Choroterpes* (*Dilatognathus*) *major* (Ulmer, 1939), **comb.n.** Ulmer distinguished imago of *major* [*Choroterpides*] from "*Choroterpides exigua*" by concavity on costal projection of hind wing [Ulmer, 1939: 498]; actually, this character can vary individually (Figs 136–137). Ulmer distinguished larvae of *major* [*Choroterpides*] from "*Choroterpides exigua*" by number of long setae on second segment of maxillary palp [Ulmer, 1939: 618]; actually, number of these setae can vary individually, being different on left and right palps of the same individual. It is unclear, if the forms, described as "*Choroterpides major*" and "*Choroterpides exigua*", belong to the same species or to different ones. Two other species of *Dilatognathus* are described as larvae — *Choroterpes* (*Dilatognathus*) *minor* (Dang, 1967 [*Choroterpides*]) **comb. n.** from Vietnam and *Choroterpes* (*Dilatognathus*) *nigella* (Kang et Yang, 1994 [*Choroterpides*]) **comb. n.** from Taiwan.

The species described as male imago from Hainan (China) under the name *Choroterpides hainanensis* You et Gui, 1995 has unclear systematic position.

Besides *Ch.* (*D.*) *cataractae* **sp.n.** and species from Java, I have examined larvae of *Dilatognathus* from Thailand and Hainan.

1.1.1.1.2.3-1. Dilatognathus/g(1) *cataractae* sp.n. [*Choroterpes*] Figs 129–133

Original binomen: *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.**
Possible binomina:
— *Choroterpes* (*Dilatognathus*) *cataractae*;
— *Choroterpes* (*Euthraulus*) *cataractae*;
— *Euthraulus* (*Dilatognathus*) *cataractae*;
— *Dilatognathus cataractae*.

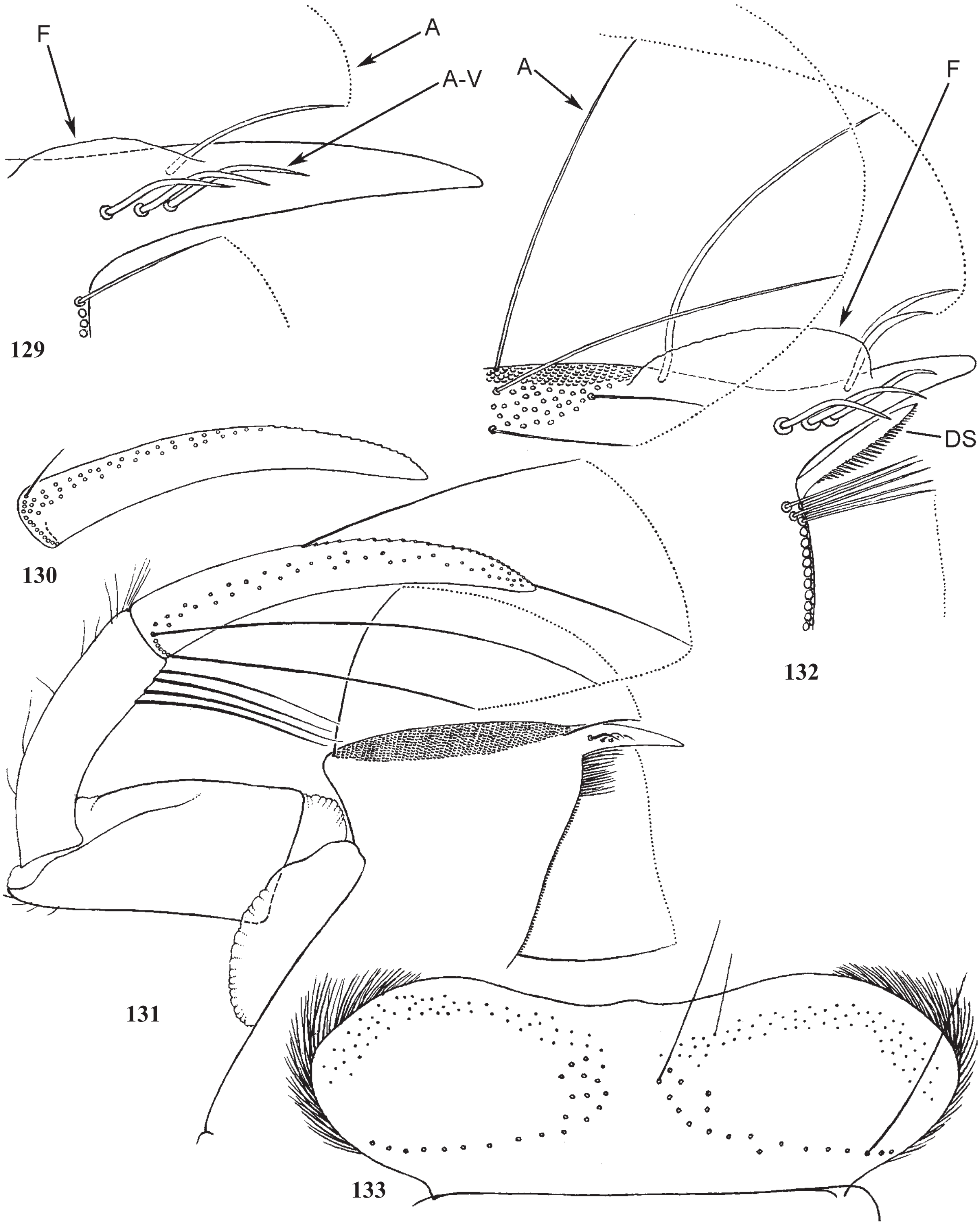
MATERIAL. Holotype: L-S-I♂ {No. [XXXIX] (6)]}, Indonesia, Lombok, Senaru, under Sendang Gila waterfall, 25.IX.2009, coll. N. Kluge & L. Sheyko. Peratypes: the same locality, 19–26.IX.2009: 3 L-S-I♂, 10 L-S-I♀, 1 L-S♂, 1 L-S♀, 49 larvae.

Larva. CUTICULAR COLORATION: Cuticle of head, pronotum and mesonotum brown, with diffusive markings; cuticle of legs and abdomen light brownish, nearly unicolorous, without contrasting markings.

HYPODERMAL COLORATION: Head and thorax with dark maculae. Fore protoptera with darkened proximal part of subcostal field. Abdomen and femora with brown pigmentation as in imago; tibiae light. Each tergalius has dorsal lamella dark brown, ventral lamella light brown.

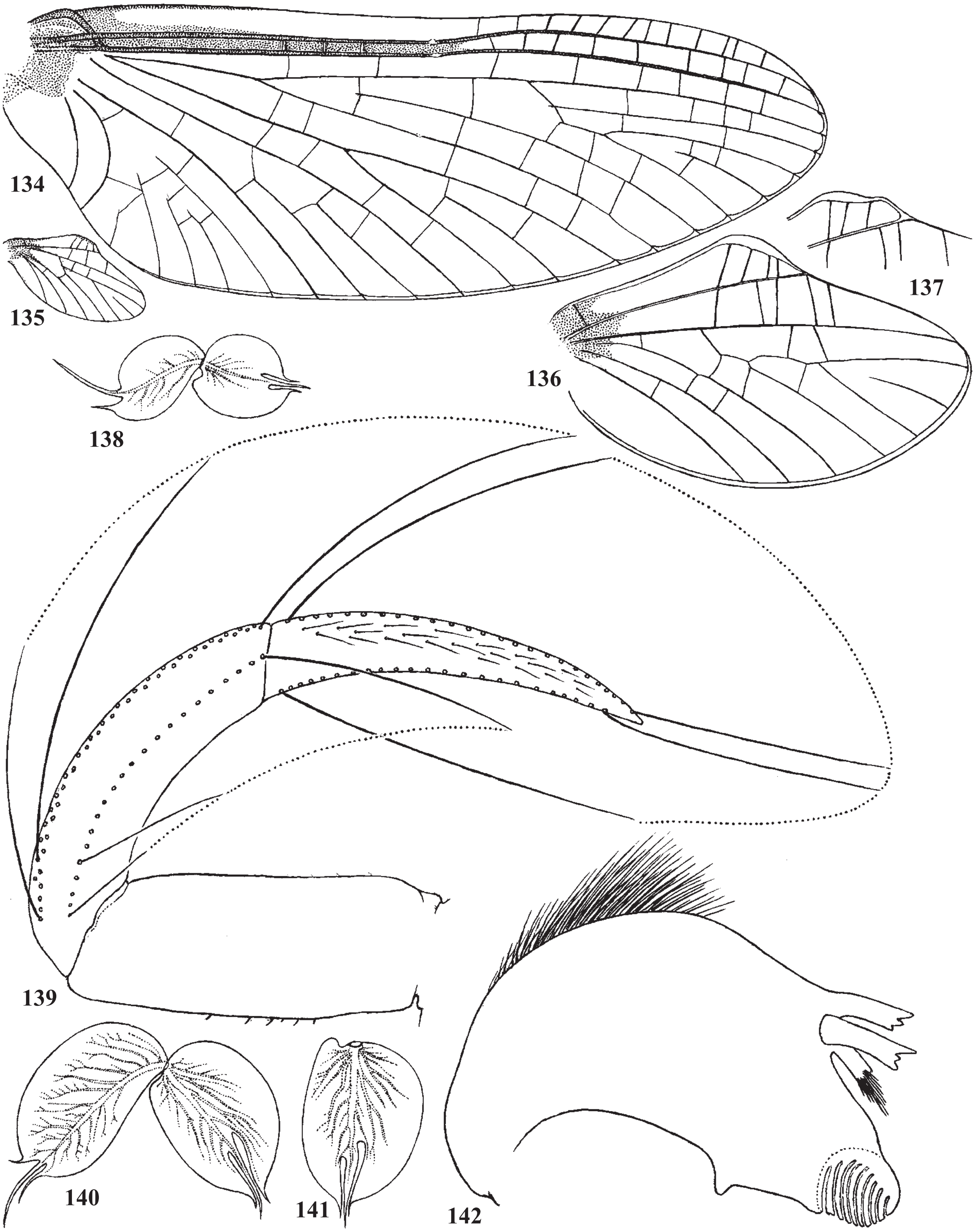
SHAPE AND SETATION: Labrum (Fig. 133) has median incision very shallow, with shallow convexity in middle, denticles not expressed; proximal transverse row of setae [shifted proximally — see *Dilatognathus* (1)] interrupted medially; instead of distal transverse row, there is a wide stripe of irregularly situated setae, smaller than setae of the proximal transverse row; most part of dorsal surface with irregularly situated long and thin setae, somewhat smaller than setae of the distal stripe (not shown in Fig. 133). Other mouthparts as in Figs 129–131, 139. Legs as in Figs 147–151: Femur of fore leg widest proximally, femora of middle and hind legs widest at middle. Femora with irregularly situated stout setae of various length; dorsal side of fore femur with a few setae, dorsal side of middle and hind femora with many setae. Ventral side of hind femur with a stripe of irregularly situated curved pectinate setae (Figs 150–151). Stout setae on inner side of fore tibia situated densely and irregularly, pointed and bipectinate (with two rows of stout pointed processes by sides). Inner side of middle and hind tibia with a sparse row of stout setae; outer side of hind tibia with stout setae of variable length, as on outer side of femur. Outer sides of all tibiae with irregularly situated thin hairs, whose length exceed tibia width (not shown in Figs 147–150). Abdomen without stout setae. Posterolateral spines short and obtuse. Hind margins of abdominal terga with very thin, spine-like denticles, whose size increases from tergum I to tergum X; lateral parts of terga I–VIII lack denticles; sterna lack denticles. Hind margins of segments of caudalii with spine-like denticles and whorls of stout setae, whose length does not exceed length of segment. Tergalii II–V have equal size and shape (Fig. 140), tergalius VI smaller, tergalius VII smallest and lacks costal process of dorsal lamella (Fig. 138); anal-proximal projection of ventral lamella poorly expressed on tergalius II (Fig. 140), better developed on tergalii III–VII (Figs 141, 138). Protogonostyli of male larva short and narrowly separated; protopenes convergent, completely hidden under sternum XI (Fig. 144). Female larva has hind margin of abdominal sternum IX slightly incised (Fig. 143).

Subimago. CUTICULAR COLORATION: Cuticle of thorax at most light with brown sclerites; mesonotum at most brown;



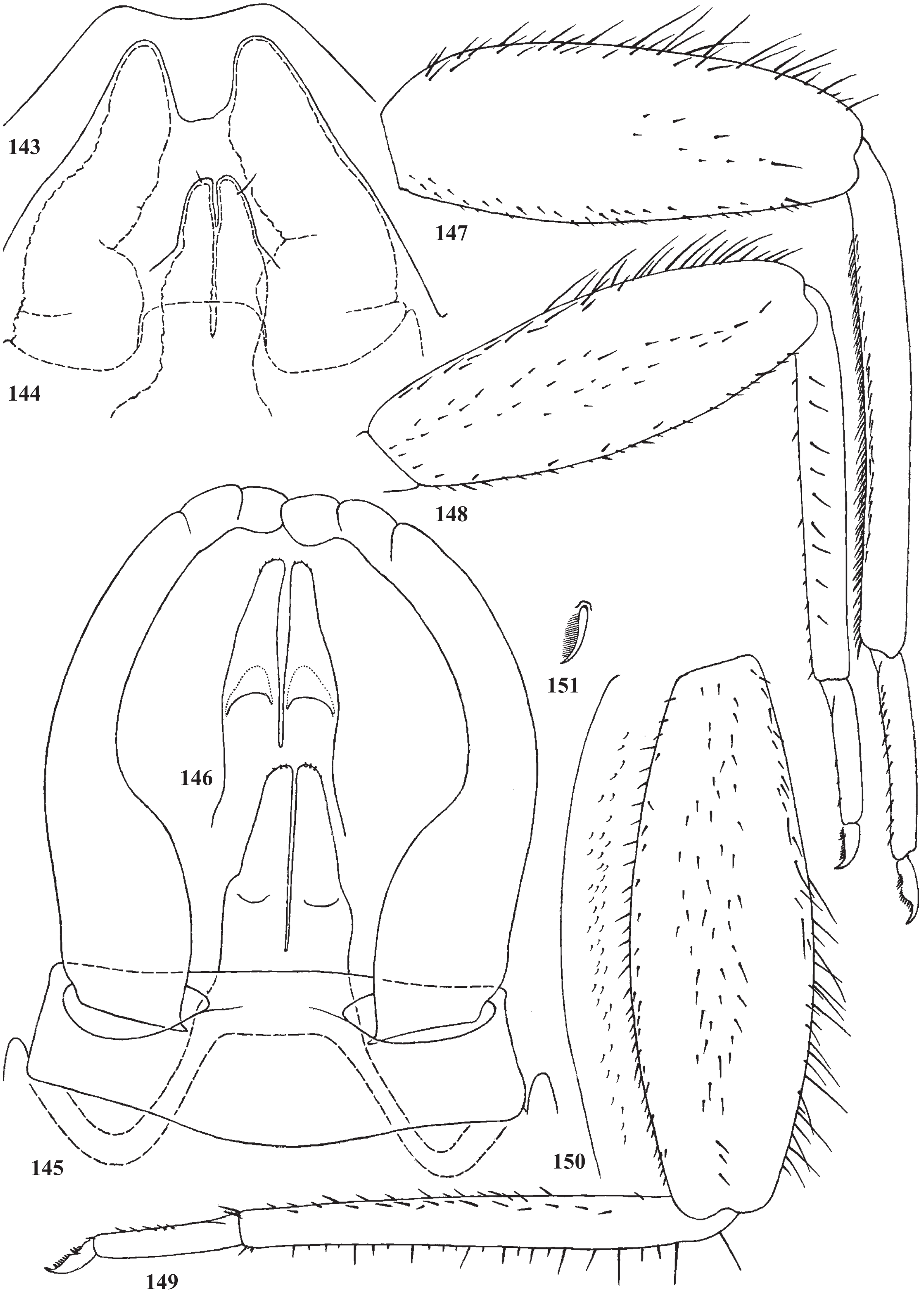
Figs 129–133. *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.**: 129–132 — maxillae (instead of most setae, only their bases and tips are shown): 129–131 — maxilla of last instar larva: 129 — apex, ventral view; 130 — 3rd segment of maxillary palp, dorsal view; 131 — ventral view; 132 — apex of maxilla of penultimate instar larva, ventral view; 133 — labrum (holotype), dorsal view (most of setae on dorsal surface not shown; bases of setae of proximal transverse row shown as rings; bases of setae of distal transverse stripe shown as dots; other setae of dorsal surface not shown).

Рис. 129–133. *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.**: 129–132 — максиллы (вместо большинства щетинок показаны только их основания и вершины): 129–131 — максилла личинки последнего возраста: 129 — вершина, вентрально; 130 — 3-й членик максиллярного щупика, дорсально; 131 — вентрально; 132 — вершина максиллы личинки предпоследнего возраста, вентрально; 133 — верхняя губа (голотип), дорсально (большая часть щетинок на дорсальной поверхности не показана; основания щетинок проксимального поперечного ряда показаны колечками; основания щетинок дистального поперечного ряда показаны точками; прочие щетинки дорсальной поверхности не показаны).



Figs 134–142. *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.**: 134–135 — fore and hind wings (holotype); 136 — hind wing; 137 — costal projection of hind wing, another specimen; 138 — tergalius VII (dorsal lamella bent to the left); 139 — labial palp, ventral view (instead of most setae, only their bases and tips are shown); 140 — tergalius II (dorsal lamella bent to the left); 141 — ventral lamella of tergalius III; 142 — left mandible.

Рис. 134–142. *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.**: 134–135 — переднее и заднее крылья (голотип); 136 — заднее крыло; 137 — костальный выступ заднего крыла, другой экземпляр; 138 — VII тергалия; 139 — нижнегубной щупик, вентрально (вместо большинства щетинок показаны только их основания и вершины); 140 — II тергалия (дорсальный листок отогнут влево); 141 — вентральный листок III тергалии; 142 — левая мандибула.


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most part of medioscutum and submedioscutum brown, posterior scutal protuberance brown except median margin (as in Fig. 92). Cuticle of legs light, with diffusive brownish stripes. Wings light brownish. Cuticle of abdominal terga light brownish; abdominal sterna I–VIII colorless; sternum IX light brownish anteriorly and laterally, with colorless semicircular area medially-posteriorly; cuticle of gonostyli light brownish.

Hypodermal coloration: Abdomen and femora with brown coloration as in imago.

Texture: On each leg 1st tarsomere (shortened and fused with tibia) covered by microtrichiae of the same shape as microtrichiae on tibia; 2nd–5th tarsomeres covered by pointed microlepides.

Imago, male. Head brown with ocher; dorsal eyes not elevated [as in Kluge, 1984: Fig.22], brownish-orange. Thorax brown with ocher. On fore wing basal part, including costal brace, and subcostal field brown, other membrane colorless; thick veins light brown, thin veins colorless; pterostigma whitish, with about 12 simple crossveins (Fig. 134). Hind wing basally brown, with costal projection blunt (Figs 135–137). Legs with brown hypodermal pigmentation: each femur dark brown in middle part, somewhat lighter brown basally and apically; tibia lighter (varies from ocher to brown), basally darker brown; tarsus either of the same color as tibia, or lighter, sometimes colorless. Abdominal terga have non-contrasting brown hypodermal coloration: each abdominal tergum at most part light brown; posterior and lateral margins darker brown; anterior margin light; a pair of submedian and a pair of sublateral light blanks are integrated with light anterior margin; each tergum I–IX has a pair of longitudinally-oval light lateral blanks, corresponding to dorsal attachments of lateral dorso-ventral muscles. Sterna I–VIII lighter, abdominal ganglia tinged with light brownish. Abdominal sternum IX has light brown cuticular coloration anteriorly and laterally; medially with grayish-brown hypodermal coloration; styliger and gonostyli light brown. Styliger with straight posterior margin. 1st+2nd segments of gonostylus with inner margin shallowly convex. Penes brown; each penis has apical projection [see Choroterpes/fg2 (3)] moderately long, conic, slightly bent medially-dorsally; its denticles are very small (Figs 145–146). Caudalii light brown, with dark brown ring at each joining.

Imago, female. Coloration as in male. Posterior plate of abdominal sternum IX apically slightly incised, as in larva (as in Fig. 143).

Egg. Yellow, oval. Chorion bears evenly dispersed papillae and ridges going from one papilla to another [see Choroterpes/fg2 (1)]; papillae small, one pole bears larger papillae.

DIMENSION. Fore wing length 7.5–8 mm.

DISTRIBUTION. Lombok Island.

COMPARISON. Male and female imagoes differ from other species by brown coloration of proximal part of subcostal field of fore wing.

1.1.1.1.2.3-2. Dilatognathus/g(1) **sp.1**

?= *Choroterpides major* Ulmer, 1939.

MATERIAL. Indonesia, Java, Cibodas (= Tjibodas), pool under waterfall at southern side of golf field, 6–11.VIII.2009, coll. N. Kluge & L. Sheyko: 23 larvae.

DISTRIBUTION. Java.

COMMENT. Nguyen & Bae [2003] reported "*Choroterpides major*" from Vietnam; diagnosis, which they gave to this species, includes only characters common for all species of *Dilatognathus*, so presence of this species in Vietnam is not proven.

1.1.1.1.2.3-3. ?Dilatognathus/g(1) **sp.2**

= "*Choroterpides exiguus*" sensu Ulmer, 1939 (non *Thraulus exiguus* Eaton, 1884).

MATERIAL. Indonesia, Java, Bogor, botanic garden, 24.II.2008, at light, coll. V. Ivanov: 2 I♂, 4 S♂, 1 S♀.

1.1.1.1.2.3-4. Dilatognathus/g(1) **sp.3**

MATERIAL. Thailand: province Mae Hong Son, river Namlang near Lot Cave, 12.I.1998, coll. V. Ivanov: 13 larvae; province Muang Pai, river Pai, 11.I.1998, coll. V. Ivanov: 7 larvae; SW Chiang Mai, Doi-Ithanon, river Klang, 17.I.1998, coll. Grigorenko: 1 larva; natrional park Kaeng Krachan, river Pchetchabun, 26.II.2006, coll. M. Chertoprud: 4 larvae.

Larva differs from *Ch.* (*D.*) *cataractae* **sp.n.** by the following features: fore femur widest near middle; tibiae with dark brown hypodermal coloration.

1.1.1.1.2.3-5. Dilatognathus/g(1) **sp.4**

MATERIAL. China, Hainan, Miao-Li, 19.XII.1957, coll. N. Andrianova: 7 larvae.

Larva differs from *Ch.* (*D.*) *cataractae* **sp.n.** by wider femora of all legs, with setae longer.

Leptophlebiid larvae with «*Dilatognathus*-type» mouthpart structure

In some non-related taxa of Atalophlebolinguata larvae independently got mouthpart structure of «*Dilatognathus*-type». These taxa are: (1) *Dilatognathus*, belonging to Choroterpes/fg2 — see above; (2) *Notophlebia* Peters & Edmunds, 1970 — Indian taxon of unclear phylogenetic position; (3) Hermanellognatha, belonging to New World taxon Hermanellonota [Kluge, 2008]; (4) Hagenulus/fg3 (= subgenus *Hagenulus* Eaton, 1882), belonging to New World taxon Hagenulus/fg2 (= genus *Hagenulus* s.l.) [Kluge, 1994]; (5) Ulmeritus/g2 (= subgenus or genus *Ulmeritus* Traver, 1956, s.str.), belonging to Neotropical taxon Ulmeritus/g1 (= genus *Ulmeritus* s.l., including *Ulmeritoudes* Traver, 1959). Some characters of their mouthpart structure are shown in Table 1.

In all these taxa labrum is widened, and its proximal setal row (characteristic for Atalophlebopectinata) is

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Figs 143–151. *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.**: 143 — outline of hind margin of abdominal sternum IX of mature female larva; 144 — larval protogonostyli and protopenis (dorsal view, shown by integral lines) with developing subimaginal genitals inside (shown by interrupted lines); 145 — genitals of male imago (ventral view); 146 — penis of another specimen (ventral view); 147–149 — fore, middle and hind legs (dorsal view); 150 — inner margin of hind femur, ventral view; 151 — seta near inner margin of hind femur; 146–151 — holotype.

Рис. 143–151. *Choroterpes* (*Dilatognathus*) *cataractae* **sp.n.**: 143 — очертание заднего края IX стернита брюшка зрелой личинки самки; 144 — протогоностили и протопенис личинки (дорсально, показаны сплошными линиями) с развивающимися субимагинальными гениталиями внутри (показаны прерывистыми линиями); 145 — гениталии самца имаго (вентрально); 146 — пенис другого экземпляра (вентрально); 147–149 — передняя, средняя и задняя ноги (дорсально); 150 — внутренний край заднего бедра, вентрально; 151 — щетинка около внутреннего края заднего бедра; 146–151 — голотип.

Table 1. Mouthparts of «*Dilatognathus*-type» in five non-related taxa
Таблица 1. Ротовой аппарат «*Dilatognathus*-type» в пяти неродственных таксонах

taxa		***Dilatognathus*** (Figs 129–133, 139)	***Notophlebia*** ult. & juv.	**Hermanellognatha** ult. & juv.	**Hagenulus/fg3** ult. & juv.	**Ulmeritus/g2** ult.
labrum	incision	wide	wide	narrow	wide	wide
	proximal row	**proximal**	**proximal**, irregular	**proximal**	**proximal**	**proximal**
mandible	outer margin	semicircular	semicircular	angulate	angulate	semicircular
maxilla	apical flange	**lost** (in young larva shortened)	**lost**	**lost**	shortened or **lost**	shortened
	dentiseta	**lost** (in young larva straight)	**lost**	**lost**	straight	**lost**
	pectinate setae	vestigial	**lost**	**lost**	present	present
	tusk	**long**, grows	**long**	from short to **long**, not grows	short or **long**, grows	**long**
	1st palpomere	**strengthened**, elongated	**strengthened**	**strengthened**, shortened	**strengthened**	**strengthened**
	$2^{nd}+3^{rd}$ palpomere	**elongated**	**elongated**	**elongated**	**elongated**	**elongated**
	long setae on 3rd palpomere	irregularly	transverse rows	transverse rows	irregularly	irregularly
labium	2nd palpomere	**elongated**, no muscles	shortened, with muscle	**elongated**, with muscle	**elongated**, no muscles	normal, no muscle
	long setae on 2nd palpomere	**longitudinal rows**	—	**longitudinal rows**	**longitudinal rows**	—
	3rd palpomere	**elongated**	**elongated**	normal	normal (short)	normal (short)
	long setae on 3rd palpomere	longitudinal rows	transverse rows	—	—	—

strongly shifted proximally; median incision of labrum can be either widened (in *Dilatognathus*, *Notophlebia*, Hagenulus/fg3 and Ulmeritus/g2) or not (in Hermanellognatha). Mandibles (whose shape is often coordinated with labrum width) are always flat and widened, with strongly convex outer margin, whose shape varies from semicircular to angulate.

Maxilla undergoes a strong modification: instead of the apical flange, the pectinate dentiseta [see Atalophlebomaxillata (1)] and the apical-ventral row of pectinate setae (characteristic for Leptophlebia/fg1 in general) (Fig. 2), its inner-apical angle gets a single long tusk. This tendency is variously expressed in various taxa. Apical flange is completely lost in *Notophlebia* and Hermanellognatha [Kluge, 2008: Fig. 37]. Among Hagenulus/fg3, the apical flange is lost in *Hagenulus morrisonae* Peters et Alayo, 1971 [Kluge, 1994: Fig. 32], while a shortened apical flange is retained in *Hagenulus caligatus* Eaton, 1882 [Peters, 1971: Fig. 152]. In *Dilatognathus* the apical flange is nearly lost in last larval instar (Fig. 129), but a shortened flange is retained in younger larva (Fig. 132). In Ulmeritus/g2 apical flange is retained, being somewhat shortened. Dentiseta (which in other Atalophlebomaxillata is curved apically — Figs 2, 4, 5) is either straight and parallel to the tusk, or absent: straight dentiseta is retained in both species of Hagenulus/fg3 [Kluge, 1994: Fig. 32] and in younger larvae of *Dilatognathus* (Fig. 132); dentiseta is completely lost in ultimolarva of *Dilatognathus* (Fig. 129), in young and old larvae of *Notophlebia*, Hermanellognatha [Kluge, 2008: Fig. 37] and at least in ultimolarva of Ulmeritus/g2 (whose younger larvae have not been examined by me). Apical-ventral row of pectinate setae is completely lost in *Notophlebia* and Hermanellognatha [Kluge, 2008: Fig. 37]; three vestigial setae, shifted to the tusk, are retained in *Dilatognathus* (Figs 129, 132); in Hagenulus/fg3 and Ulmeritus/g2 the pectinate setae are retained [Kluge, 1994: Fig. 32; Peters, 1971: Fig. 152; Dominguez, 1991: Fig. 9], being smaller, than in related taxa. Tusk is present in all these taxa, but its size varies. Particularly, in *Dilatognathus* the tusk grows from instar to instar, being in ultimolarva very long (Figs 129, 131); among Hagenulus/fg3, *Hagenulus caligatus* has tusk short [Peters, 1971: Fig. 152], while in *Hagenulus morrisonae* tusk grows from instar to instar, being in ultimolarva very long [Kluge, 1994: Fig. 32]. In Hermanellognatha the tusk seems not to change proportions from instar to instar; in some taxa of Hermanellognatha (e.g., all species of *Traverella* Edmunds, 1948) the tusk is small; in some others very long [Kluge, 2008: 37]. Some authors used length of the tusk as a generic character and established genera *Hydrosmilodon* Flowers & Dominguez, 1992 and *Hydromastodon* Polegatto et Batista, 2007 for species of Hermanellognatha with especially long tusks. However, long tusks of the same shape independently evolved in several species of Hermanellognatha-Needhamella/g1 and in one of two species of Hermanellognatha-Hylister/g(1) [Kluge, 2008].

Maxillary palp always has elongated 2nd and 3rd segments taken together. Its 3rd segment always bears very long filtering setae, which are situated either irreg-

ularly (in Hagenulus/fg3, Ulmeritus/g2 and *Dilatognathus* — Figs 130, 131), or form many short regular transverse rows (in *Notophlebia* and Hermanellognatha) [Kluge, 2008: Fig. 37]. The 1st segment (which bears muscles moving the second segment) is thickened and strengthened; it can be either shortened (e.g., in Hermanellognatha), or, vice versa, elongated (e.g., in *Dilatognathus* — Fig. 131).

Labium always has paraglossae widened and strongly expanded laterally [Peters & Edmunds, 1970: Fig. 165, 171; Peters, 1971: Figs 143, 144; Dominguez & Flowers, 1989: Figs 46, 59, 70, 81; Dominguez, 1991: Fig. 13]. Labial palp can be either non-modified (in Ulmeritus/g2), or modified as filtering, in addition to filtering maxillary palp. In this case its 2nd and 3rd segments taken together are elongated and bear long filtering setae. But ways, how this effect is reached, vary among taxa: in *Dilatognathus* both 2nd and 3rd segments are elongated and bear longitudinal rows of filtering setae (Fig. 139); in Hagenulus/fg3 only 2nd segment is elongated and bears longitudinal rows of filtering setae, while 3rd segment is short, as in all Hagenulus/fg2 [Kluge, 1994: Fig. 25]; in *Notophlebia*, vice versa, 2nd segment is strongly shortened and lost setation, while 3rd segment is strongly elongated and bears numerous transverse rows of filtering setae.

Thus, in five non-related taxa the same combination of mouthpart modification occurs: (1) labrum and mandibles are widened; (2) on labrum proximal transverse row of setae is shifted proximally; (3) inner-apical angle of maxilla is more or less simplified and strengthened; (4) maxillary palp gets this or that filtering specialization; (5) paraglossae of labium are widened; (6) labial palp can get this or that filtering specialization. Adaptive role of this combination of mouthparts modification is unclear.

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